The Systematics and Evolution of the *Oenothera caespitosa* Species Complex (Onagraceae)

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The Systematics and Evolution of the *Oenothera caespitosa* Species Complex (Onagraceae)

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Robert E. Stockhouse
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The cover illustration is *Oenothera caespitosa* subsp. *caespitosa*; see Fig. 102.

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Abstract

The *Oenothera caespitosa* group consists of five closely related species in western North America. All five are diploid ($n = 7$), except for uncommon tetraploids ($n = 14$) in *O. caespitosa*. The complex has diversified principally through two processes. The first pattern, represented by the polymorphic *O. caespitosa*, is characterized by ecological and geographical diversification without substantial concomitant genetic divergence. The second process involves ecological shifts to specific and extreme habitats and further is characterized by fundamental morphological changes that are often accompanied by chromosomal reorganization and perhaps plastid differentiation.

The first pattern of diversification has led to the evolution of the five largely allopatric subspecies of *O. caespitosa* that all share a basic chromosome arrangement and are able to form fully viable and fertile hybrids. Natural hybridization occurs in areas where the subspecies are sympatric or probably were in the past. New forms arising through hybridization appear to have made possible the continued survival of this species in the rapidly changing arid habitats of the western United States. This phenomenon has served to weaken or diminish the distinctness between the subspecies by the production of series of intermediate populations.

The other four species have evolved by very different kinds of processes. Each species is geographically and edaphically restricted and is sharply distinct from *Oenothera caespitosa* from which each was independently derived. *Oenothera cavernae* from the Grand Canyon area and *O. brandegeei* from central Baja California have switched from the perennial to annual habit accompanied by the loss of self-incompatibility and the shift to predominant autogamy. Furthermore, the evolution of at least *O. brandegeei* has involved structural rearrangement of the chromosomes via reciprocal translocations. *Oenothera harringtonii* of southeastern Colorado has also switched to the annual habit while *O. psammophila*, a dune specialist in Idaho, although perennial, has undergone substantial morphological shifts including the development of a sand sheath to protect tender young growth from damage by blowing sand. Moreover, the plastids of *O. psammophila* may have differentiated relative to those of *O. caespitosa*.

A cladistic analysis suggests that the *Oenothera caespitosa* complex is a monophyletic group most closely related to *O. primiveris*, a species of the low desert regions of the southwestern United States and northern Mexico, and *O. xylocarpa*, an endemic to volcanic substrates in the southern Sierra Nevada of California and Nevada. These three lineages are related to *O. muelleri*, a species known only from a few isolated mountain-tops in Nuevo León, adjacent Tamaulipas, and Coahuila Mexico.

The analysis suggests that *O. caespitosa* is a paraphyletic grouping and that three of the other four species were each independently derived from different elements of *O. caespitosa*. Evidence is presented to suggest that *Oenothera psammophila* probably was derived following hybridization of *O. caespitosa* subspp. *caespitosa* and *marginata*.

The divergence of the *Oenothera caespitosa* group and the other three lineages to which it is related appears to have been closely linked to the Pliocene spread of dry climate. The subsequent diversification of the *O. caespitosa* complex in more recent times is a process that is still in a very active stage.

Introduction

Oenothera, with about 123 species assigned to approximately 14 sections, is the largest genus in the specialized tribe Onagreae and the second largest after *Epilobium* in the Onagraceae. Although its species are widely distributed in temperate North and South America, *Oenothera* attains its greatest diversity in western North America, where approximately 60 species in 14 sections occur. *Oenothera* is well known for the extensive experimental research performed mostly on species of sect. *Oenothera* subsect. *Oenothera*. This classical work, summarized by Cleland (1972), has spanned well over 70 years and has involved numerous workers. Early investigations centered on the meiotic chromosomal behavior associated with complex structural heterozygosity. More recent studies of this genus have led to new insights into plastid evolution (e.g., Stubbe, 1964; Stubbe & Raven, 1979), the genetics and physiology of self-incompatibility (e.g., Emerson, 1938; Crowe, 1955; Dickinson & Lawson, 1975), and genetic variation in populations (e.g., Levy & Levin, 1975; Levy & Winterheimer, 1977).

Despite these extensive studies, a complete modern systematic treatment of the entire genus has yet to be realized. In 1930 P. A. Munz initiated a revisionary series in *Oenothera* as part of his lifelong studies of New World Onagraceae. Munz (1930, 1931a, 1931b, 1932, 1935, 1937, 1949, summary 1965) used a conservative approach and brought a remarkable degree of order to a genus that earlier had been greatly confusing taxonomically. More recently, a series of modern systematic studies were initiated involving an investigation of crossing relationships, cytology, and examination of variation within and between populations in the field. Work has been completed for sect. *Oenothera* subsect. *Munzia* (Dietrich, 1977), subsects. *Raimannia* and *Emersonia* (Dietrich et al., 1985), and subsect. *Oenothera* (Raven et al., 1979; Dietrich & Wagner, in prep.); sect. *Kneiffia* (Straley, 1977), sects. *Lavauxia*, *Megapterium*, and miscellaneous small sections (Wagner, in prep.); sects. *Anogra* and *Kleinia* (Klein, in prep.); sect. *Hartmannia* (Raven et al., in prep.); and the present paper on part of sect. *Pachylophus*. Taken together, these papers will constitute a modern biosystematic review of the entire genus.

Oenothera sect. *Pachylophus* has received relatively little attention. Only Munz (1931b, 1965) and Raven (1970) made taxonomic contributions to our understanding of sect. *Pachylophus* during the past 50 years. Munz included five species: *O. caespitosa* Nutt., *O. cavernae* Munz, *O. xylocarpa* Coville, *O. primiveris* A. Gray, and *O. tubifera* Sér. Within the *Oenothera caespitosa* group as defined here, Munz recognized one species with 11 varieties (1931b). Primarily because only a limited number of herbarium specimens were available to him, his taxonomy included several taxa now recognized as artificial. In 1965, Munz treated the *Oenothera caespitosa* group as one species with nine subspecies, a classification he considered tentative. Subsequently, Raven (1970) considered the relationships of *O. muelleri* Munz and *O. macrosceles* A. Gray to the five species included by Munz in sect. *Pachylophus*. He also raised *Oenothera brandegeei* of central Baja California, where it is disjunct from the remainder of the *O. caespitosa* group, to specific level. Later, Stockhouse (1973) initiated a study of the cytology, crossing relationships, and pollination biology of the *O. caespitosa* group. The results of his study that are pertinent to the classification or interpretation of the evolution of the group are included here. The present study

was initiated in order to derive an improved taxonomy for the *Oenothera caespitosa* complex. Further we were interested in gaining some insight into understanding how the entities diverged from one another and how they are presently maintained. Finally, we desired some knowledge of the relationship of the taxa to one another and to the rest of the genus.

Information about isolating mechanisms, natural hybridization, and variation patterns were obtained from the examination of natural populations. Seeds collected from natural populations were grown for hybridization to study the crossing relationships of certain taxa. This work was augmented by the study of over 6,000 herbarium specimens representing over 2,000 collections from throughout the range of the group. In addition to the comparative morphological study of characters historically used to distinguish taxa in this group, many new characters were investigated. Especially useful was a study of the external and internal morphological features of seeds with the scanning electron microscope. Finally, the more formal and objective methods of cladistics were utilized to formulate hypotheses of relationships among the taxa and their relationship to the remainder of the genus. The group as presented in the systematic treatment consists of five closely related species, one of which, *Oenothera caespitosa,* is highly polymorphic and is divided into five broadly defined subspecies.

Ecology and Geography

The *Oenothera caespitosa* group occurs in western North America from southern Alberta and Saskatchewan south through the Rocky Mountains and Basin and Range regions to extreme northern Chihuahua, Mexico, and to Trans-Pecos Texas. Plants are typically scattered, often in small populations, in desert scrub, pinyon-juniper woodland, or coniferous forests, usually in open, rocky or unstable sites. Some of the taxa, in particular *O. caespitosa* subspp. *marginata, macroglottis,* and *caespitosa* often colonize roadcuts and other recently disturbed sites if there is an available source of seed in contiguous areas. Among the kinds of sites most frequently occupied by members of the group are steep rocky slopes, scree, outcrops, heavy clays, arroyo margins, recent alluvium, and the periphery of harvester ant mounds.

The range of *Oenothera caespitosa* encompasses nearly the full geographical and ecological range of the group. Four of its subspecies are ecologically well separated from one another and their ranges overlap only to a limited extent. *Oenothera caespitosa* subsp. *crinita* grows on limestone and dolomite from northern Nevada and Utah west of the Wasatch Range south to the Inyo region of California. It consists of two forms: the common form ranges from Mojave Desert scrub to pinyon-juniper woodlands throughout the region, whereas the pulvinate form, which has a highly condensed habit and spreads into large mats, has a discontinuous range in the southern part of the overall range of the subspecies with one highly disjunctive station on sandstone ledges on the Red Plateau, near Woodside, Emery County, Utah. The ecological distribution of the pulvinate form is also highly interrupted. It occurs at high elevations on exposed limestone and marble with bristlecone pine (*Pinus longaeva* D. K. Bailey) and at much lower elevations in pinyon-juniper woodland on chalky white limestone. This geographical and ecological distribution suggests that the pulvinate form may have been much more widespread in the past and became restricted to its present distribution only recently. A number of other taxa exhibit very similar altitudinal and edaphic patterns including the bristlecone pine, *Pinus longaeva* (Bailey, 1970) and the *Lesquerella hitchcockii* Munz–*L. tumulosa* (Barneby) Reveal species pair (Reveal, 1979).

Oenothera caespitosa subsp. *navajoensis* is restricted to the Colorado Plateau, mostly in xeric scrub to pinyon-juniper woodland. It grows on fine-textured sandstones and clays that sometimes have high gypsum content.

Oenothera caespitosa subsp. *macroglottis* grows on mostly igneous substrates in the southern Rocky Mountains in open sites in upper elevations of pinyon-juniper woodland, ponderosa pine–Douglas fir forest, and sometimes spruce-fir forest. There are disjunct stations in the Abajo Mountains of southeastern Utah and the Sandia and Manzano Mountains in central New Mexico. Spreading dry climate during the last 10,000 years and the relatively low dispersibility of plants of this group taken together suggest that these stations may be relicts of a wider distribution attained during the pluvial periods of the Pleistocene. In western Colorado the ranges of subspp. *macroglottis* and *navajoensis* overlap, but these entities are elevationally and edaphically distinct.

The widely distributed *Oenothera caespitosa* subsp. *caespitosa* occupies the northernmost geographical area of the complex. It occurs primarily on shale and heavy clays from northern Nevada and eastern Oregon in sagebrush (*Artemisia* spp.) to conifer forests east through the northern and middle Rocky Mountains in coniferous forests, out onto the northern Great Plains to North and South Dakota primarily in open heavy clay sites. This extensive range overlaps with the ranges of subsp. *crinita* in northern Nevada, subsp. *macroglottis* in northern Colorado and adjacent Wyoming, and extensively with subsp. *marginata* throughout the southwestern third of the range of subsp. *caespitosa*. In each of these regions of overlap the taxa are ecologically isolated, largely because of the substrate differences indicated above. However, sporadic hybrids or relatively uniform populations thought to be ultimately of hybrid origin occur in each of the regions of geographical overlap.

Oenothera caespitosa subsp. *marginata* is the most widely distributed and common entity in the complex, occurring in some part of every western state except Montana. It is very diverse ecologically. It occurs primarily on limestone in California, parts of Arizona, and New Mexico; on volcanic cinders in parts of Arizona, Utah and Idaho; on sandstones in the Colorado Plateau region, or occasionally on finer textured substrates such as shales in Colorado, and even on gypsum in Arizona and New Mexico. Although subsp. *marginata* centers in pinyon-juniper woodlands, it occurs in a variety of other vegetation types including Arizona chaparral along the margin of the Sonoran Desert, ponderosa pine forest (mostly southern parts of the range), big sagebrush scrub (Great Basin), and grasslands (southeastern Arizona, adjacent New Mexico and Chihuahua).

The range of *Oenothera caespitosa* subsp. *marginata* overlaps, sometimes extensively, with that of each of the other four subspecies. In these areas of overlap they are always ecologically isolated, either edaphically (subsp. *caespitosa*), or primarily altitudinally (subsp. *macroglottis* and the common form of subsp. *crinita*), or both (subsp. *navajoensis*). Despite this isolation, hybrids or populations of presumed hybrid origin exist in each area of geographical overlap. For example, in Inyo County, California, both subspp. *crinita* and *marginata* are common in the limestone mountains. *Oenothera caespitosa* subsp. *marginata* is found at middle elevations of the mountains in canyons and on slopes, whereas the common form of subsp. *crinita* occurs together, with hybrids between it and subsp. *marginata*, at lower elevations on the bajadas in Mojave Desert Scrub up to pinyon-juniper woodland. The pulvinate form of subsp. *crinita* occurs near the mountain summits in exposed sites at elevations well above those at which populations of subsp. *marginata* occur, and also at much lower elevations in extremely dry, rocky limestone sites that are edaphically quite distinct from those occupied by adjacent populations of subsp. *marginata*. Another example of predominantly altitudinal separation is that between subspp. *marginata* and *macroglottis* in western Colorado, where populations of one subspecies gradually take on the characteristics of the other along an altitudinal gradient. In contrast, subspp. *navajoensis* and *caespitosa*, both of which occur on fine-textured soils, are sharply distinct edaphically from subsp. *marginata*, which is characteristic of more coarsely textured soils. *Oenothera caespitosa* subsp. *marginata* is even more fully isolated from subsp. *navajoensis*, because subsp. *marginata* occurs in more mesic sites at higher elevations.

The other four species in the *Oenothera caespitosa* group are geographically restricted edaphic specialists. *Oenothera cavernae* is the most widespread, occurring in xeric desert scrub throughout the Grand Canyon region on steep rocky limestone slopes or along sandy desert washes. Populations are also known in and around the low calcareous mountains of Clark County, Nevada. *Oenothera harringtonii* is restricted to silty clay soils in the foothill grasslands along the Front Range in southeastern Colorado. The remaining two species are each known from much more restricted areas. *Oenothera brandegeei* is known only from two localities in central Baja California, Mexico: one above Bahía de los Angeles on the mainland, and one from Isla Angel de la Guarda just to the east in the Golfo de California. It grows among volcanic rocks in an area of less than 100 mm of erratically distributed rain per year. This habitat is by far the most xeric in which any member of the *O. caespitosa* group occurs. It is also separated by more than 600 km from the nearest populations of the closely related *O. caespitosa* subsp. *crinita* in San Bernardino County, California, and over 800 km from the nearest populations of a pulvinate form of subsp. *crinita* which *O. brandegeei* may be considered to be most closely related. The last

species, *O. psammophila,* is restricted to a single large area of shallow drifting sand dunes over a basement of lava in Fremont County, southeastern Idaho.

Breeding Systems, Pollination, and Dispersal

breeding systems and pollination

Observations and collections of pollinators in Colorado, Utah, and Idaho were made by Stockhouse (1973) and in Arizona, Colorado, and California by Gregory (1963, 1964). Further details on nectar content of flowers and pollinator activity are provided by Stockhouse (1973). Stockhouse also analyzed flowers for the presence of ultraviolet-reflecting patterns. Pollen was stained with cotton blue in lactophenol. Percentages of stainable pollen were based on counts of 600 grains.

Self-compatibility was determined in the greenhouse for at least three plants from each population. The flowers were selfed, and put in insect-proof cages for 48 hr. Styles were collected after 24–48 hr. and placed in a saturated solution of potassium iodide. Pollen tubes in *Oenothera* are lined with starch grains, which accept the iodine and can be seen in the style as dark, granular beads, or threads (Renner, 1919). Styles were examined for pollen tube penetration. Plants that did not set seed following numerous attempts, as well as those in which the pollen tube failed to penetrate the stigma were classified as self-incompatible. All plants set a full complement of seed when pollinated with pollen from another individual in the same population. Plants were classified as self-compatible only if seed was regularly set following self-pollination.

There are two types of breeding systems in the *Oenothera caespitosa* complex. All wild plants have high pollen stainability generally ranging from 85–95% stainable pollen; this conclusion is based on 35 populations studied in the field. *Oenothera caespitosa, O. psammophila,* and *O. harringtonii* are self-incompatible and are outcrossed primarily by several species of hawkmoth visitors (Sphingidae). As is characteristic for Onagraceae as a whole, the self-incompatibility system is gametophytic (Raven, 1979). In *O. caespitosa* subsp. *marginata,* it involves at least five S-alleles (Bills, 1968). In *Oenothera,* pollen-tube growth is inhibited in the surface layers of the stigma (Bills, 1968; Dickinson & Lawson, 1975). The remaining two species of the group, *O. cavernae* and *O. brandegeei,* are self-compatible and normally autogamous, as evident by observations of self-pollination in the absence of any potential pollinators in the greenhouse; they have much smaller flowers than do their outcrossing relatives.

The flowers, with the exception of the much smaller ones of the autogamous *Oenothera cavernae* and *O. brandegeei,* have characteristics associated with vespertine pollination by hawkmoths. The outcrossing species have floral tubes 3–6 cm or up to 16 cm long in some individuals of *O. caespitosa* subspp. *marginata* and *macroglottis,* while the two autogamous species have floral tubes 0.5–4.7 cm long. The odor of the flowers in the outcrossing species is sweet and moderately strong, with a background rubbery scent in the perennials *O. caespitosa* and *O. psammophila* and a somewhat stronger gardenia-like scent in the annual *O. harringtonii.* The flowers of the two autogamous species are essentially scentless. Flowers of all of the species open during the hour following sunset and are available for pollination until the following morning when they fade in direct sunlight. The petals have moderate to weakly ultraviolet reflective areas over the entire surface, with no sharply contrasting patterns. This pattern is consistent with that of other hawkmoth-pollinated Onagraceae such as *Calylophus* (cf. Towner, 1977).

Although the spectrum of the hawkmoth visitors to populations of the *Oenothera caespitosa* group differs somewhat from night to night depending on weather conditions (Stockhouse, 1973), the overall range of visitors was rather constant in any particular geographical area. Observations of visitors are summarized in Table 1 and photographs of the moths are presented in Figures 1–7. *Hyles lineata* is the most common pollinator in the group essentially throughout its range. In decreasing order of frequency of visitation, *Sphinx vashti, S. asella, S. chersis,* and *Manduca quinquemaculata,* all hawkmoths with tongues ranging from 6 to 14 cm long, were the most common pollinators of the longer floral-tubed taxa (floral tube lengths 4.5–16.3 cm), *O. caespitosa* subspp. *marginata* and *macroglottis.* The frequency of these larger moths is greater at moderate to higher elevations where subspp. *marginata* and *macroglottis* occur. Both of these subspecies have floral tubes that are exceedingly variable in length: individuals of subsp. *marginata* from the southern parts of its range have longer tubes than those from farther north,

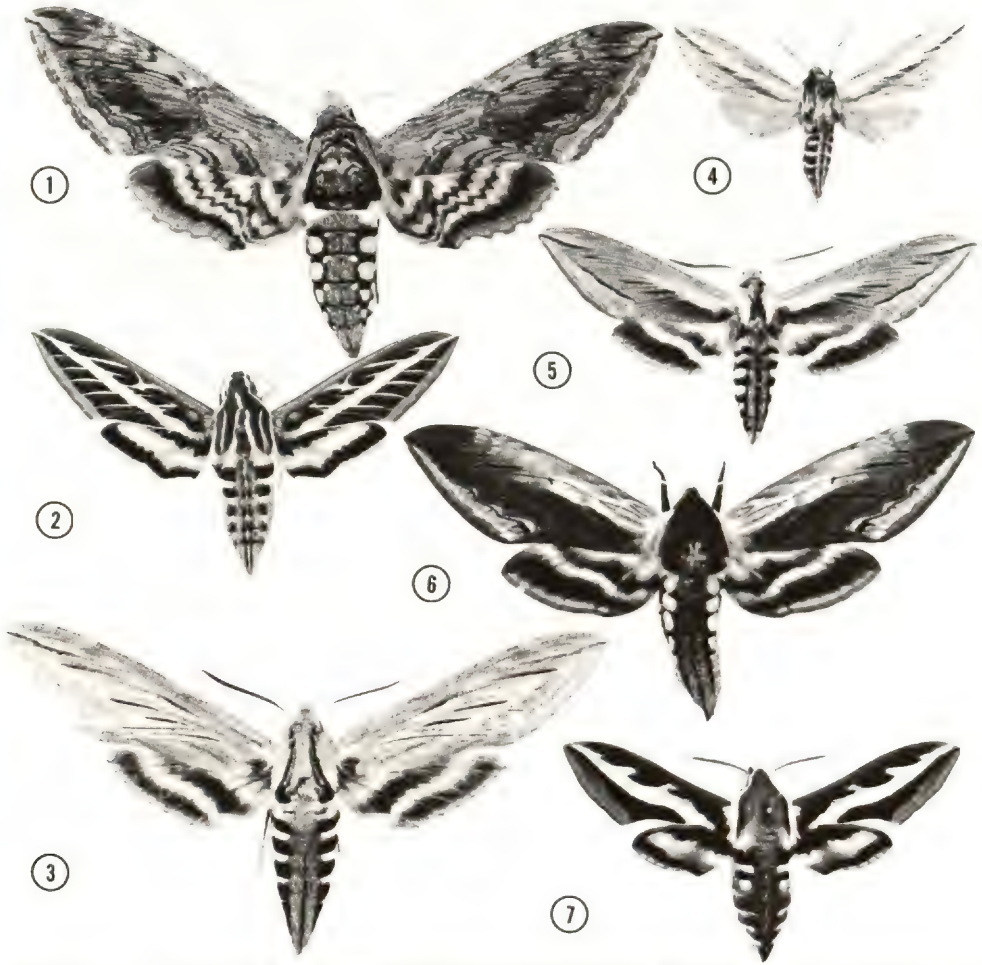
TABLE 1. Pollinators of the *Oenothera caespitosa* group.

Taxon	Locality	Number of Populations Studied	Investigator	Insect Visitors
O. caespitosa				
Subsp. *crinita*	Inyo Co., California	1	Gregory, 1964	*Hyles lineata* (Fabricius)
Subsp. *macroglottis*	Larimer Co., Colorado	5	Stockhouse, 1973	*Sphinx vashti* Strecker, *S. chersis* (Hubner), *Manduca quinquemaculata* (Haworth)
	Montezuma Co., Colorado	1	Gregory, 1964	*Sphinx chersis, Manduca quinquemaculata, Hyles lineata*
	San Juan Co., Utah	1	Stockhouse, 1973	*Sphinx vashti, S. chersis, Manduca quinquemaculata*
Subsp. *marginata*	Coconino Co., Arizona	2	Gregory, 1964	*Sphinx asella* (Rothchild & Jordan), *S. chersis, S. dolli* Neum., *S. drupiferarum* J. E. Smith, *Hyles lineata*
	Inyo Co., California	1	Gregory, 1964	*Hyles lineata*
	Fremont Co., Idaho	1	Stockhouse, 1973	*Sphinx* spp., *Manduca quinquemaculata*
	Clark Co., Nevada	4	Gregory, 1964	*Hyles lineata*
O. psammophila	Fremont Co., Idaho	2	Stockhouse, 1973	Noctuids, *Hyles lineata, H. gallii* (Rottenburg)

whereas, the variation in subsp. *macroglottis* exhibits no apparent pattern. This variation, at least in subsp. *marginata*, is presumably related to the abundance of long-tongued and short-tongued pollinators, a pattern first suggested for *Oenothera* by Gregory (1964). Details of the pattern of floral tube variation in each of these subspecies are given in the systematic treatment. *Oenothera psammophila* is pollinated by both *Hyles* species but apparently more commonly by noctuid species. No observations have yet been made of pollinators at the strongly scented flowers of *O. harringtonii*.

The behavior of *Sphinx* spp. and *Manduca quinquemaculata* when visiting the flowers of *Oenothera caespitosa* subsp. *macroglottis* was fairly consistent. The moths generally hovered, inserted their proboscis, and then landed on the wide nearly horizontal floral platform which is composed of the petals. They often effect pollination as their proboscis, legs, or body brush the stigma. The three *Sphinx* species with their medium length (4–7 cm) tongues (Gregory, 1964) thrust their head and body deep into the floral tube in an effort to suck up as much nectar as possible. In *O. caespitosa* subsp. *macroglottis* they frequently plunge so deep that only their wingtips protrude above the floral platform. *Manduca* with long tongues (12–14 cm; Gregory, 1964) can withdraw most of the nectar without inserting its head into the floral tube.

The frequency of hawkmoth visits to *Oenothera caespitosa* subsp. *macroglottis* flowers was observed to depend directly upon three environmental factors; wind, precipitation, and air temperature. Of the three, air temperature was the most important. Hawkmoth activity was greatest on warm nights. As the temperature dropped below 15°C, hawkmoths became very scarce, and at temperatures below approximately 12–14°C, they were not observed at all. These data agree with laboratory experiments conducted with *Manduca sexta* (L.) by Heinrich (1971) who found that *M. sexta* was unable to generate sufficient



FIGURES 1–7. Hawkmoth (Sphingidae) pollinators of the *Oenothera caespitosa* group.—1. *Manduca quinquemaculata.*—2. *Hyles lineata.*—3. *Sphinx chersis.*—4. *Sphinx dollii.*—5. *Sphinx vashti.*—6. *Sphinx drupiferarum.*—7. *Hyles gallii.*

thoracic temperature to fly at temperatures below approximately 12°C. Hawkmoths were absent from all populations on nights when the wind velocity was high or gusting sporadically, as in advance of local thundershowers. Periods of light rain had little effect on hawkmoth activity on warm evenings. No hawkmoths were observed after heavy rainstorms.

In addition to hawkmoth pollinators, a number of bee species visit the flowers of the *Oenothera caespitosa* group. These bees are primarily early-morning visitors to the flowers, scavenging pollen still available at that time. Many of the bee species are oligolectic, collecting pollen only from species of Onagraceae (Linsley et al., 1963). Most of these species do not effectively pollinate the large-flowered hawkmoth-adapted species like *Oenothera,* owing to their size and behavior coupled with the wide separation of stigma and anthers in these species (Linsley et al., 1963).

The following species were observed by Linsley et al. (1963) in their study of the behavior of bees and the Onagraceae in the Great Basin. Two polylectic bees, *Lasioglossum* (*Lasioglossum*) *sisymbrii* (Cockerell) and *L.* (*L.*) *trizonatum* (Cresson), have been observed collecting pollen in the early morning in Colorado on *O. caespi-*

TABLE 2. Capsule and seed production in the *Oenothera caespitosa* group.

Taxon	Number of Capsules Produced per Stem	Number of Seeds per Capsule
O. caespitosa		
Subsp. *crinita*	0–7(–12)	(20–)30–90
Subsp. *caespitosa*	3–6(–25)	30–110
Subsp. *navajoensis*	4–25(–32)	50–115
Subsp. *macroglottis*	2–4(–8)	80–140
Subsp. *marginata*	1–3(–15)	75–170
O. psammophila	(1–)3–4(–10)	50–90
O. harringtonii	6–20	60–100
O. cavernae	1–40	5–80
O. brandegeei	1–30	1–30

tosa subsp. *macroglottis*. At least the latter species probably does not collect a significant amount of its pollen from *Oenothera caespitosa* except under conditions of pollen shortage. Two other native bees, both oligolectic, have been observed on *Oenothera caespitosa* subsp. *macroglottis* in Colorado. *Andrena* (Onagrandrena) *anograe knowltoni* Linsley & MacSwain visits *Oenothera* flowers in the early morning; this bee species is known to collect pollen only from species of *Oenothera* with large white flowers (*Oenothera caespitosa* and *Oenothera* sect. *Anogra*). In contrast *Lasioglossum* (*Sphecodagastra*) *texanum* (Cresson) is nocturnal and has been observed at the flowers of *O. caespitosa* subsp. *macroglottis* in Colorado. *Apis mellifera* L., the honeybee, also has been observed to collect pollen occasionally from the flowers of *Oenothera caespitosa*.

Two other bee species, *Lasioglossum* (*Evylaeus*) *aberrans* (Crawford) and *L.* (*E.*) *galpinsiae* (Cockerell), were collected at a Larimer County, Colorado locality. Both were observed to collect pollen from *Oenothera caespitosa* subsp. *macroglottis*, primarily in the early mornings. *Lasioglossum galpinsiae* is oligolectic, collecting pollen from *Oenothera, Gaura,* and *Camissonia* (Linsley et al., 1963).

On six successive evenings during the summer of 1971, an experiment was conducted by Stockhouse (1973) at a population in Larimer County, Colorado, to determine if these bees were effective in pollinating *Oenothera caespitosa* subsp. *macroglottis*. Fifty percent of the flowers were bagged each night to exclude hawkmoths. The remaining flowers were allowed to open and were visited by hawkmoths. At 5:30 A.M. the following morning, the bags were removed from those flowers that had been covered, and bees were seen shortly thereafter, actively collecting pollen. Capsules were marked on all flowers and were collected 1–1.5 months later. Only one out of 150 of the flowers that were visited only by bees set capsules. Approximately 70% of the flowers that were hawkmoth-pollinated produced capsules. Therefore, hawkmoths were responsible for virtually all of the pollination that occurred in the study population of *O. caespitosa* subsp. *macroglottis*. In general, bees are pollen robbers at the flowers of normally hawkmoth-pollinated species of *Oenothera,* including *O. caespitosa,* and seem to play no significant role in the pollination of these plants (cf. Linsley et al., 1963; Gregory, 1964).

DISPERSAL

Seed production. Capsule and seed production is quite variable. Most of the taxa produce relatively few mature capsules (Table 2), each with about 50–100 seeds each. There are, however, some notable differences among the taxa. Of the perennials, *Oenothera caespitosa* subsp. *crinita* generally produces the fewest mature capsules, and this is particularly true of the pulvinate form when it occurs at high elevations. Its relatively low seed set may be related to the lower frequency of hawkmoths at higher elevations (Cruden et al., 1976). The pulvinate form does, however, reproduce vegetatively. It produces large pulvinate mats that undoubtedly live for considerable periods of time. Similarly, *O. caespitosa* subsp. *macroglottis* normally produces only 2–4 mature capsules, but each of its capsules has up to about 140 seeds. It also reproduces vegetatively by forming colonies of rosettes from adventitious shoots from the roots. Subspecies *marginata, caespitosa,* and *navajoensis,* although variable, produce more capsules, often up to 30 on a single stem. In addition, subsp. *marginata* produces larger capsules than the other taxa except subsp. *macroglottis*; both have up to about 150 seeds in each capsule. *Oenothera harringtonii,* and apparently also *O. psammophila,* consistently produce moderate numbers of capsules: 8–10 and 3–4 per stem respectively. Finally, the two autogamous annuals, *O. cavernae* and *O. brandegeei,* are exceedingly variable both in seed and in capsule production, this is perhaps dependent for the most part on the amount of available moisture.

Seed release and dispersal. Seed dispersal in the *Oenothera caespitosa* group over ecological time is apparently rather limited. During their evolutionary history, however, the group has spread nearly throughout western United States presumably by gradual dispersal into adjacent new suitable habitats as they became available. Some of these habitats, such as pinyon-juniper woodland, have occupied much larger and more continuous areas in the past than they occupy now. Dispersal in the group is largely due to four mechanisms. First, the capsules of most of these species only dehisce along part of their length, and thus many seeds are retained at the site of the maternal plant. This retention is enhanced when the tardily dehiscent capsules become buried as soil collects around the bases of the plants. In *O. caespitosa* subsp. *navajoensis* and subsp. *caespitosa* the capsules dehisce up to three-quarters of their length, and *O. psammophila* has capsules that dehisce nearly throughout their entire length. Thus, the number of seeds released ranges from roughly two-thirds or more in *O. psammophila* to about one-fourth of the total seed production in three subspecies of *O. caespitosa.*

The seeds retained in the capsules, as mentioned before, often become buried in the soil that collects around the maternal plant. Occasionally, these seeds have been observed to germinate inside the capsule, but more often the entire capsule and the contained seeds ultimately disintegrate in the soil without ever producing any new plants. The capsules do eventually become detached from the plants, and may be dispersed.

Seed dispersal in *Oenothera cavernae* is generally very restricted. The capsules dehisce one-third to one-half their length at maturity allowing about half of the seeds to be dispersed. The remainder are retained in the highly lignified lower portion of the capsules which does not disintegrate until the next wet season. The capsules also remain firmly attached to the rooted dead plant. In the course of several rainy periods the tissues slowly disintegrate allowing a few seeds to fall out directly around the maternal plant. In March 1979, several populations of *O. cavernae* were examined by Wagner in Clark County, Nevada; in all cases an old maternal plant was surrounded by seedlings or flowering individuals. Occasionally a new plant grew between two closely spaced capsules or out of one of the capsules on the maternal plant. Thus, most dispersal was within a few centimeters to perhaps several decimeters. Fruiting material of *L. brandegeei* collected by Reid Moran on Isla Angel de la Guarda illustrates that the capsules in that species are nearly indehiscent, splitting only at the very top, and so the two autogamous annual species of the *O. caespitosa* group are similar in this respect. Similar patterns in which the plants have mechanisms restricting the dispersal of its seeds occur in many desert annuals (Went, 1979). Went suggests that the dead maternal plant provides favorable microhabitat by providing a site for water retention as well as providing nutrients from the decaying tissues.

A second dispersal mechanism is that of water dispersal. Seeds that fall to the ground in the immediate area of the maternal plant may be washed to greater distances by water during thunderstorms either in arroyos or by sheet flooding. This may be a particularly effective mechanism since the seed-collars (see p. 16) provide very effective flotation prior to their filling with water after a day or so under moist conditions.

Myrmecochory is another effective dispersal mechanism in certain populations of *Oenothera caespitosa* subsp. *navajoensis* in *Atriplex* scrub and grasslands in western Colorado and eastern Utah. These plants commonly form rings at the margin of harvester ant (*Pogonomyrmex* sp.) mounds (Fig. 8). This phenomenon was brought to our attention in 1979 by W. A. Weber and by K. A. Pirozynski and D. W. Malloch, based on their independent observations in this area. In 1980, Wagner examined a population at Highline Lake, Grand County, Colorado, and confirmed that *Oenothera* plants grow almost exclusively around the periphery of harvester ant mounds and that the ants actively collect their seeds. Empty seed coats as well as whole seeds were common in the mound material and inside the nests of two mounds which were dug up and the material carefully sifted under a dissecting microscope. *Oenothera caespitosa* subsp. *navajoensis* seeds made up less than 10% of the total seeds collected by the ants. It was, however, the only perennial species strongly associated with the mounds. Three or four other species made up the bulk of the seeds found in the nest. These species, including *Hilaria jamesii* (Torrey) Benth. and *Astragalus asclepiadoides* Jones, more generally are common in the area, and are not especially associated with the ant mounds. Wheeler (1910), while discussing plant colonization on

FIGURE 8. *Oenothera caespitosa* subsp. *navajoensis* growing on the periphery of harvester ant [*Pogonomymnmex occidentalis* (Cresson)] mound 6.4 km N of Rangely, Rio Blanco County, Colorado. Photograph taken by W. Weber, May 1979.

the periphery of ant mounds, illustrated his point with a photograph of an unidentified plant growing in a large ring around a harvester ant mound at Las Vegas, New Mexico. The plant in the photograph, based on flower size, habit, and locality, could only have been *O. caespitosa* subsp. *macroglottis*. *Oenothera caespitosa* subsp. *marginata* has also been observed to be associated with harvester ant mounds in Fremont County, Idaho (Gordon Whitehead, pers. comm.).

A final mechanism of seed dispersal in this group involves small rodents. Rodents have been observed carrying capsules of *Oenothera caespitosa* subsp. *caespitosa* in Boulder County, Colorado, and those of subsp. *marginata* in the foothills of the Charleston Mountains, Clark County, Nevada. Because of the extremely tough texture of the capsules and the retention of some seeds in their basal portion, it appears unlikely that rodents would eat all of the seeds, and in this way some would be dispersed. At the present time, our knowledge of rodent dispersal in this group does not go beyond these observations.

MORPHOLOGY

The morphological characters used in the evaluation of relationships and phylogeny will receive a more formal treatment in a later section devoted to those topics. Here morphology is discussed in general terms without considering which characters constitute homologues or which are plesiomorphic (original or pre-existing) or apomorphic (derived). Measurements were made primarily on dried herbarium specimens, although observations on living materials were incorporated when they were available.

Morphology and internal features of seeds were examined by scanning electron microscopy (SEM). Viable seeds were attached to aluminum stubs with Archers plastic cement (Rollins, 1955), coated with 500–700 Å of gold in a sputter coater, and examined in a Hitachi S-450 SEM at 15 kV and 60–80 μA. Photomicrographs were made with Type 55 P/N Polaroid film. Contact prints were made on Ilford No. 4 paper. Seed surface features are presented at roughly 30×, 250×, and 1,000× magnifications. Internal features were examined by slicing living seeds and photographing them at various magnifications between 30× to 1,000×. Unless otherwise indicated, the photomicrographs of seed surfaces at higher magnifications were taken on the abaxial surface of the seed since this surface consistently exhibited more conservative morphology than the lateral or adaxial surfaces. In all, 17 populations are presented as representative of the range of vari-

TABLE 3. Voucher information[a] for seeds of species of *Oenothera* illustrated in scanning electron micrographs, Figures 1–72.

Oenothera brandegeei: Mexico, Baja California, *Moran 12983.*
O. caespitosa subsp. *caespitosa:* U.S.A., Colorado, Routt Co., *Wagner 4044*; Idaho, Lemhi Co., *Hitchcock et al. 3698*; Oregon, Wheeler Co., *Wagner 4466.*
O. caespitosa subsp. *crinita:* U.S.A., Nevada, Clark Co., *Wagner 4494*; Nye Co., *Beatley 9291*; Utah, Garfield Co., *Wagner 4505*; Millard Co., *Welsh & Atwood 9682.*
O. caespitosa subsp. *macroglottis:* U.S.A., Colorado, La Plata Co., *Wagner 4514*; Boulder Co., *Wagner 4023.*
O. caespitosa subsp. *marginata:* U.S.A., Arizona, Gila Co., *Fletcher 4241*; New Mexico, Sandoval Co., *Wagner et al. 4401.*
O. caespitosa subsp. *navajoensis:* U.S.A., Utah, Grand Co., *Wagner 4509, 4510.*
O. cavernae: U.S.A., Nevada, Clark Co., *Wagner 3998.*
O. harringtonii: U.S.A., Colorado, El Paso Co., *Stockhouse 137.*
O. macrosceles A. Gray: Mexico, Durango, 17.7 mi. SW of F. I. Madero, *Wagner & Solomon 4316* (MO).
O. primiveris subsp. *bufonis* (M. E. Jones) Munz: U.S.A., Nevada, Clark Co., 10 mi. E of Glendale, *Maguire & Blood 4446* (UTC).
O. psammophila: U.S.A., Idaho, Fremont Co., *Wagner 4061.*
O. xylocarpa Cov.: U.S.A., California, Mono Co., Sierra Nevada, Smoky Bear Flat, *DeDecker in 1979* (MO).
O. muelleri Munz: Mexico, Coahuila, Rincón de María, *Wendt, Lott & Riskind 1289* (MO).

[a] Specific locality and institution(s) where specimens are deposited are given in treatment, unless indicated here.

ation in the *O. caespitosa* group. Additional samples of the four species most closely related to the *O. caespitosa* group are also illustrated for comparison, especially for out-group comparisons in the phylogenetic analysis. Vouchers for the collections of seeds illustrated in this paper are listed in Table 3. In addition, seeds from over 250 populations from throughout the geographical range of each of the taxa were examined with a dissecting scope at 50× to be sure that the full range of variation in the group was being considered.

Habit. Two species, *Oenothera cavernae* and *O. brandegeei,* are small winter annuals of the Mojave and Sonoran Deserts. A third, *O. harringtonii,* is a robust, leafy, facultative annual of grassland habitats just to the east of the Colorado Front Range. It apparently occasionally overwinters and flowers for a second season. The other two species, *O. psammophila* and the polymorphic *L. caespitosa,* are perennials.

Stems. As is predominant in the genus, all species of the *Oenothera caespitosa* group begin growth as a rosette, but prior to the cessation of flowering, most form at least rudimentary stems. *Oenothera brandegeei, O. caespitosa* subsp. *macroglottis,* and the common form of *O. caespitosa* subsp. *crinita* are usually acaulescent, and only rarely form short stems up to 4–8 cm long. *Oenothera caespitosa* subsp. *caespitosa* is more variable in this respect, varying at times in single populations from acaulescent to having stems to 10 cm long. Plants of *Oenothera caespitosa* subspp. *marginata* and *navajoensis* also may be acaulescent, but more often have ascending stems over 10 cm long with definite internodes. These stems may elongate exceptionally up to 40 cm in subsp. *marginata.* The remaining taxa have various kinds of further specializations from the more generalized ascending stem. *Oenothera harringtonii* has robust, leafy, erect stems commonly 20–30 cm long. *Oenothera psammophila* also has robust stems, but they are decumbent and become buried in the drifting sands of its dune habitat, leaving only the more erect rosette-like cluster of leaves at the tip exposed. The stems of *O. psammophila* are further specialized in that they produce numerous secondary shoots from the buried leaf axils. *Oenothera cavernae* typically produces numerous, but very short, ascending stems. *Oenothera cavernae* may produce a single rosette with very few leaves under severe conditions. The most striking stem modification is that of the pulvinate form of *O. caespitosa* subsp. *crinita* which is usually multi-branched with stems 6–14 cm long, but these arise from a buried caudex leaving only rosettes exposed at the ground surface. Finally, *O. caespitosa* subspp. *marginata, caespitosa,* and the pulvinate form of subsp. *crinita* often produce small buds at the numerous leaf scars on the older portions of the stem. This portion of the stem is often buried and one to several of these buds will elongate, typically in the spring, producing a new rosette.

The numerous secondary stems of *O. psammophila* probably represent a further specialization.

Roots. A sparsely branched somewhat fleshy taproot is characteristic of members of the *Oenothera caespitosa* group and most of the genus. Three of the subspecies of *O. caespitosa*, subspp. *macroglottis, navajoensis,* and *caespitosa,* also reproduce vegetatively by means of adventitious shoots from rather slender lateral roots. The first two of these subspecies are more vigorous, and nearly always produce colonies of rosettes up to about 1 m or more in diameter by this means. *Oenothera caespitosa* subsp. *caespitosa* reproduces in this way as well, but apparently less frequently. New shoots may be produced from roots in a number of other sections of *Oenothera* including *O. muelleri* (sect. *Pachylophus* sensu lato), *O. maysillesii* Munz (sect. *Oenothera* subsect. *Emersonia*), *O. brachycarpa* A. Gray (sect. *Megapterium*), *O. acutissima* Wagner (sect. *Lavauxia*), and *O. centauriifolia* (Spach) Steud. (sect. *Lavauxia*). In other species, including *O. speciosa* Nutt. (sect. *Xylopleurum*) and *O. pilosella* Raf. (sect. *Kneiffia*), new shoots are produced from extensive rhizomes. The overall distribution of both of these forms of vegetative reproduction in the genus is in need of careful study.

Leaves. The basic leaf shape or outline in lobed leaves is oblanceolate, although some of the taxa have modally distinctive shapes. Although some populations of *O. caespitosa* subsp. *navajoensis* have oblanceolate leaves, most populations have leaves with a severe reduction in the lower portion of the blade making the overall shape rhombic-obovate. *Oenothera caespitosa* subsp. *macroglottis* has spatulate leaves. Some populations of *O. caespitosa* subsp. *crinita* have obovate leaves with the blade usually somewhat reduced below, but more often plants of this taxon, especially in the pulvinate form, have linear-oblanceolate leaves. The narrowest leaves in the group occur in some populations of *O. caespitosa* subsp. *caespitosa* from Colorado and Wyoming with linear leaves as narrow as 3 mm.

Leaf length and lobing patterns are exceedingly variable, and are not, in general, of much diagnostic use. Leaf lengths do, however, fall into two classes. *Oenothera caespitosa* subspp. *marginata* and *macroglottis* usually have at least some leaves in the range 15–30 cm or rarely somewhat longer. This is also sometimes the case in subsp. *caespitosa,* but it never has leaves longer than 22 cm. The remaining taxa have leaves that are normally under 15 cm long with the following exceptions: rarely longer in *O. cavernae,* up to 19.5 cm; *O. caespitosa* subsp. *caespitosa,* up to 22 cm; and subsp. *crinita,* up to 17.5 cm. These differences in leaf length have been useful in detecting hybrids, especially between subsp. *marginata* and the other subspecies of *O. caespitosa* except for subsp. *caespitosa.*

Lobing patterns, because they are so variable, are not consistently useful in delimiting the taxa; nevertheless, certain of the lobing patterns are at least modally distinctive. The leaves of *O. cavernae* are most distinctive: in them, larger lobes typically alternate with smaller ones, a character that, although present in other taxa such as *O. caespitosa* subspp. *crinita* and *macroglottis,* reaches its greatest development in *O. cavernae.* In this respect, it resembles *O. primiveris.* Another distinctive lobing pattern is the narrow lobes, angled forward, in *O. brandegeei.* The regularity of the lobing is also useful in separating some taxa. *Oenothera harringtonii* has evenly dentate leaves and, while some plants of *O. caespitosa* subsp. *marginata* also have dentate leaves, but at least some of the lobes in subsp. *marginata* are of different sizes and are unevenly spaced. Both *O. caespitosa* subspp. *caespitosa* and *macroglottis,* have irregularly lobed leaves, but only subsp. *macroglottis* has smaller lobes or teeth (usually two) that alternate with larger ones, whereas subsp. *caespitosa* has teeth of uniform size. Sometimes subsp. *caespitosa* has irregularly sized teeth.

Splotches of reddish purple pigment occur on the mature leaves of *O. cavernae,* on those of some Arizona and California populations of *O. caespitosa* subsp. *marginata,* and on the cotyledons or first leaves of *O. brandegeei* and *O. caespitosa* subsp. *navajoensis.* A distinctive reddish hue is characteristic of the mature leaves of *O. cavernae,* and a similar reddish tint, also has been observed in the young leaves of some individuals of *O. caespitosa* subsp. *crinita.*

Pubescence. Hair types provide excellent diagnostic characters for the *Oenothera caespitosa* group. In addition, presence or absence of hairs is of value in some cases. Density, by contrast, is rarely useful. There are two basic hair types in the *O. caespitosa* group, glandular and nonglandular. The nonglandular types are present in all of the taxa of this group. The types of hairs can be characterized as follows:

1) *Glandular*—tiny erect transparent, blunt-tipped or clavate hairs 0.1–0.2 mm long that

exude a drop of fluid. Glandular hairs are found in all taxa except *O. caespitosa* subsp. *caespitosa* and are also absent in glabrous populations of *O. caespitosa* subsp. *macroglottis*. They may occur on any part of the plant, but are especially prevalent on the ovary and outside of the floral tube.

2) *Hirsute*—usually long unicellular hairs, (0.3–)0.6–2.2 mm long, mostly straight, erect or sometimes somewhat spreading, translucent to white with a slightly broadened base. These hairs sometimes arise from a reddish purple pustule in *O. cavernae* and in one Arizona population of *O. caespitosa* subsp. *marginata*. Hirsute pubescence is typically of variable length on any individual, and this class as represented in each individual normally includes both the longest and shortest hairs present in a given taxon. The individual ranges of this hair type for the taxa are broadly overlapping; *O. cavernae* and *O. brandegeei* (0.3–0.8 mm), *O. caespitosa* subsp. *crinita* (0.5–1.5 mm), subsp. *marginata* (0.3–2.2 mm), and subsp. *macroglottis* (0.4–1.6 mm). The last taxon has hairs that are often somewhat crinkly but not quite so much as to be grouped with *O. caespitosa* subsp. *navajoensis* as villous.

3) *Hirtellous*—similar to the hirsute pubescence but the hairs are more slender and are not perceptibly broadened at the base. This hair type is found only in *Oenothera harringtonii*. These hairs are more uniform in length on individual plants than is usually the case for the hirsute type. On different plants the hairs range from 0.6–1 mm long.

4) *Villous*—similar to hirtellous in being slender and not broadened at the base, but more twisted, often becoming tangled and then giving a shaggy appearance, especially on the buds and leaves. Villous pubescence also resemble the crinkly hirsute pubescence of *O. caespitosa* subsp. *macroglottis,* but are longer and more slender. Pubescence in some populations of *O. caespitosa* subsp. *crinita* from western Utah approaches a villous condition.

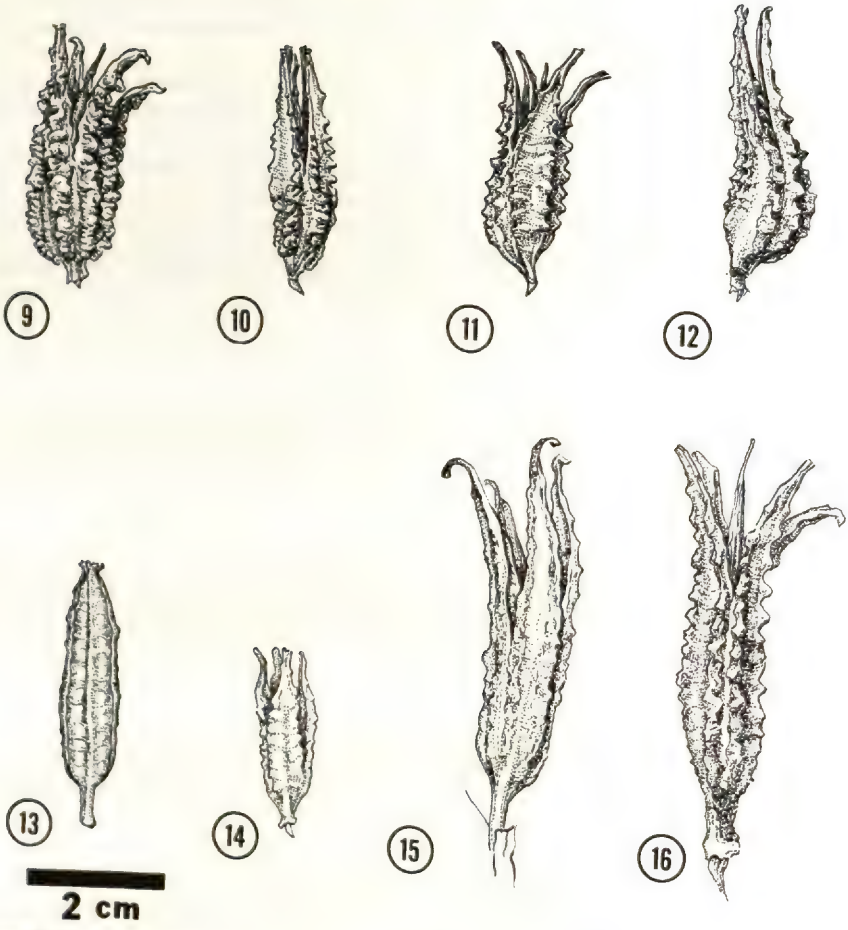
5) *Strigillose*—appressed or occasionally somewhat spreading, thickish, white, unicellular hairs 0.2–0.6 mm long, somewhat broadened at the base. Only *Oenothera caespitosa* subsp. *caespitosa* has strigillose pubescence. These appressed hairs should not be confused with the slender more appressed hairs 0.1–0.5 mm long common in many species of other sections such as *O. brachycarpa* or *O. primiveris*. These taxa, unlike those of the *O. caespitosa* group, have hirsute type mixed with the appressed ones. Hybrids between a hirsute plant (*O. caespitosa* subsp. *marginata*) and strigillose plant (*O. caespitosa* subsp. *caespitosa*) had only one intermediate hair type rather than both hair types. This result suggests that the strigillose pubescence of *O. caespitosa* subsp. *caespitosa* represent a modification of hirsute pubescence and may not be homologous with the strigillose pubescence in other sections.

Oenothera psammophila is glabrous, as are some plants of *O. caespitosa* subsp. *caespitosa* and subsp. *macroglottis*. *Oenothera psammophila* is unique in that the young leaf surface as well as other parts, such as buds, exudes a very viscid fluid which causes sand to adhere to the young parts as a kind of a sand sheath.

Flowers. Flowers in members of the *O. caespitosa* group are borne singly in the axils of the leaves, as they are in most sections of the genus. In most of the taxa, the flowers occur among the rosette leaves or along the stem in caulescent individuals or taxa. Typically one to three flowers are produced per day, although exceptionally robust individuals of *O. caespitosa* subsp. *marginata* may produce up to ten. Only *O. harringtonii* differs somewhat from this pattern, and it only in degree, producing 5–10 flowers per day along the robust stem. This increase in the number of flowers gives the impression of a terminal leafy spike.

Despite considerable variation, floral tube lengths fall into three groups: (1) Most of the self-incompatible outcrossing taxa have floral tubes 3–7(–8.5) cm (*Oenothera caespitosa* subspp. *crinita, caespitosa,* and *navajoensis, O. psammophila,* and *O. harringtonii*). (2) *Oenothera caespitosa* subspp. *marginata* and *macroglottis* have exceedingly variable floral tubes 4.5–14(–16.5) cm. This is presumably related to the broader pollinator spectrum in these two subspecies. (3) In the autogamous *O. cavernae* and *O. brandegeei* the floral tubes are reduced to 0.5–4.7 cm long.

The buds of the *Oenothera caespitosa* group are all quadrangular. Pigmentation of the buds is, however, diagnostic. The veins of the buds in most of the taxa are usually reddish purple in color. Occasionally, in *O. caespitosa* subsp. *macroglottis* or subsp. *caespitosa,* the buds are reddish throughout. Reddish purple splotches or dots consistently occur on the sepals of *O. cavernae.* They are also sometimes present on buds and ovaries in *O. caespitosa* subsp. *crinita,* and on

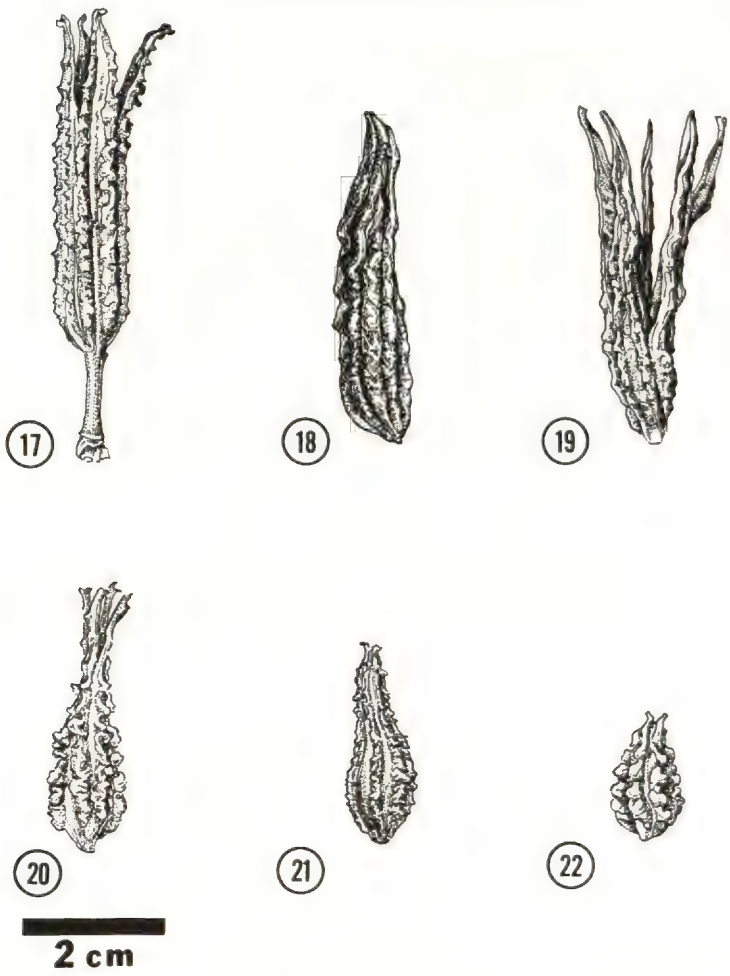


FIGURES 9–16. Mature capsules of *Oenothera caespitosa*.—9, 10. subsp. *crinita*, common form, Nye Co., NV, *Beatley 9291* (NTS).—11. subsp. *crinita*, pulvinate form, Garfield Co., UT, *Wagner 4505*.—12. subsp. *caespitosa*, Fremont Co., WY, *Stockhouse 134*.—13. subsp. *navajoensis*, isotype, Kane Co., UT, *Cronquist 10202* (DS).—14. subsp. *navajoensis*, Grand Co., UT, *Wagner 4509*.—15. subsp. *macroglottis*, Boulder Co., CO, *Wagner 4023*.—16. subsp. *marginata*, Sandoval Co., NM, *Wagner et al. 4401*. All specimens at MO unless indicated otherwise.

the buds in certain populations of subsp. *marginata* from Arizona, California, Utah, and Idaho.

The taxonomically most useful feature of the petals is the color to which they fade during the day after anthesis. When pressed and dried as herbarium specimens, they tend to change further to a somewhat more intense purple or lavender. The faded colors range from rose purple (*Oenothera caespitosa* subsp. *caespitosa* and the common form of subsp. *crinita*), through rose or pale rose (the pulvinate form of *O. caespitosa* subsp. *crinita* and some populations of subsp. *macroglottis*), to pink in the remaining taxa. Petal sizes of all species are extremely variable even within a population.

Capsules (Figs. 9–22). Despite a great amount of variation in characters of the fruit in most of the taxa, capsules provide many of the best diagnostic features in the *Oenothera caespitosa* complex. Capsules in this group are thick-walled and rather woody at maturity. They have rows of tubercles or a ridge along the margin of each valve and taper to a sterile beak at the apex. Overall shapes range from elliptic-ovoid (*O. cavernae* and the common form of *O. caespitosa*



FIGURES 17–22. Mature capsules of the *Oenothera caespitosa* group.—17. *O. caespitosa* subsp. *marginata*, Lincoln Co., WY, *Wagner 4057a.*—18, 19. *O. psammophila*, Fremont Co., ID, *Wagner 4061.*—20. *O. harringtonii*, El Paso Co., CO, *Stockhouse 137.*—21. *O. cavernae*, isotype, Clark Co., NV, *Munz 16376.*—22. *O. brandegeei*, isotype, Baja California, Mexico, *Palmer 582* (US). All specimens at MO unless indicated otherwise.

subsp. *crinita*), lanceoloid to ovoid (*O. harringtonii, O. brandegeei, O. caespitosa* subsp. *caespitosa*, and the pulvinate form of subsp. *crinita*), and lance-cylindrical (*O. psammophila, O. caespitosa* subsp. *macroglottis*, and some individuals of subsp. *marginata*), to cylindrical (*O. caespitosa* subsp. *marginata*) or oblong-lanceoloid (*O. caespitosa* subsp. *navajoensis*). In most taxa the capsules are exceedingly variable in length. The ultimate length is affected by the number of ovules fertilized, but apparently also by the environmental stresses encountered by that plant during capsule development. Nevertheless, the taxa can be divided into two modally distinctive groups based on fruit length. Many of the taxa range from about 1 to 3.5 cm (in *O. caespitosa* subsp. *navajoensis* up to 4 cm). The second group overlaps with the first, but capsules in it are, in general, longer. This group includes *O. psammophila* (3–4.7 cm), *O. caespitosa* subspp. *caespitosa* (1–5 cm), *macroglottis* (1.7–5.6 cm), and *marginata* (2–6.8 cm). *Oenothera caespitosa* subspp. *crinata, caespitosa, O. brandegeei*, and *O. cavernae* all have falcate or sigmoid capsules, at least before maturity, as do the related species *O. primiveris* and *O. xylocarpa* outside the group. In

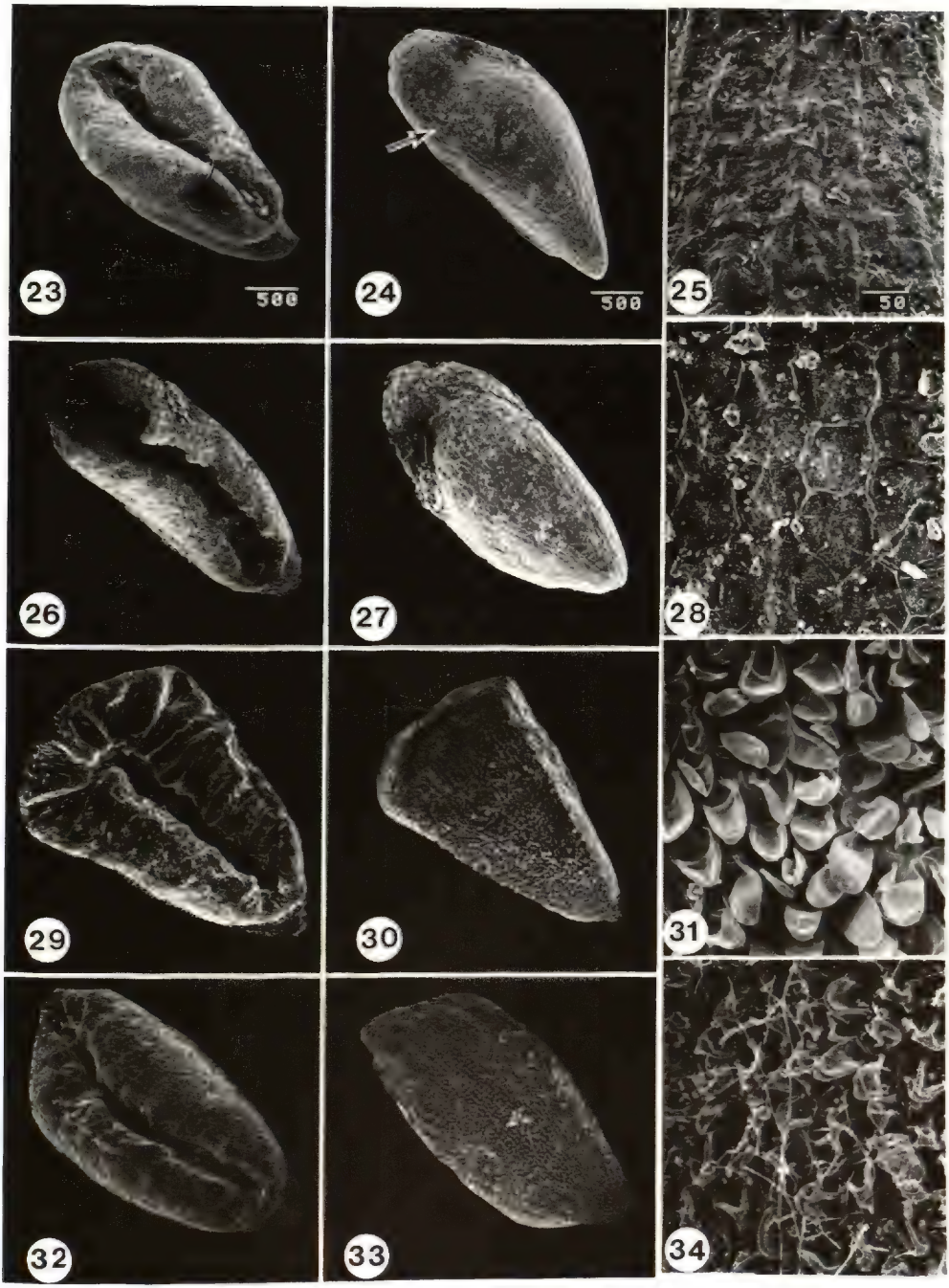
contrast, *O. caespitosa* subspp. *marginata* and *navajoensis* and *O. harringtonii* have essentially straight capsules, whereas *O. psammophila* and *O. caespitosa* subsp. *macroglottis* have intermediate, slightly curved capsules. The capsules in *O. psammophila* are unique in being somewhat twisted.

Some of the taxa have asymmetrical capsules. This asymmetry is caused by a bulging on one side of the capsule near the base. The distribution of asymmetrical capsules roughly parallels the distribution of falcate capsules with the exception that *O. caespitosa* subspp. *navajoensis* and *macroglottis* have somewhat asymmetrical capsules that are not falcate. Furthermore, the capsules of *O. caespitosa* subspp. *crinita, caespitosa,* and to some degree *macroglottis* are also flattened perpendicular to the bulge, a feature that enhances the asymmetry of the capsule. Pedicels in the *L. caespitosa* group are typically very short, ranging from 0.5–2 mm and are strongly flattened. *Oenothera cavernae* and *O. brandegeei,* however, have subsessile capsules, although sometimes in *O. cavernae* the capsules produced late in the season may have a pedicel up to 1 cm long under conditions of capsule crowding. *Oenothera harringtonii,* rather than having an actual pedicel, has a broad constriction at the base of the capsule roughly half the capsule diameter. In contrast, *O. caespitosa* subsp. *macroglottis* often has pedicels 4–7 mm long and subsp. *marginata* has the greatest variation with pedicels ranging from the typical few millimeters to over 5 cm.

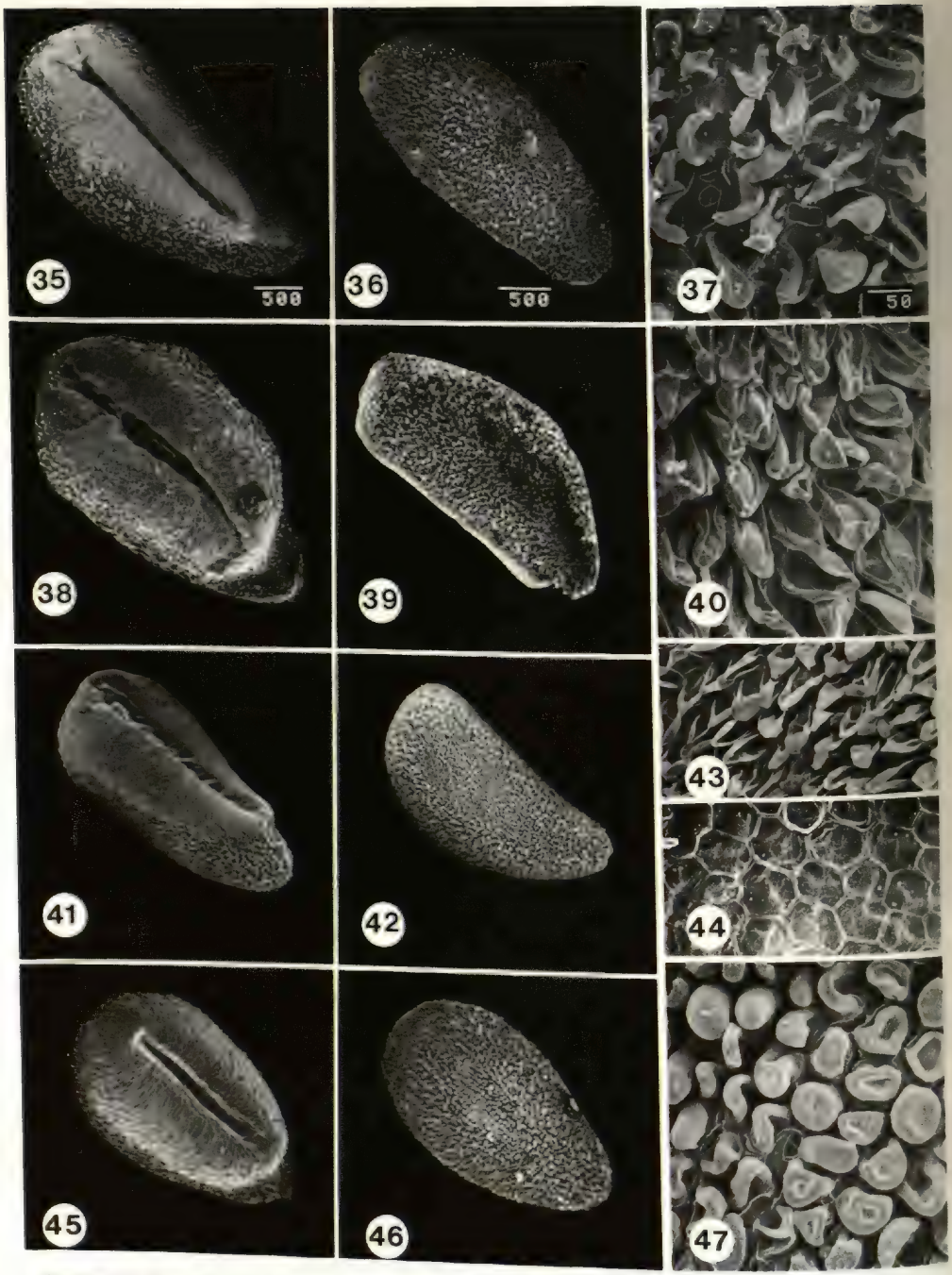
The size, number, and degree of coalescence of the tubercles are quite variable, in some instances even within populations. Some features of the tubercles are, however, useful. *Oenothera brandegeei* has few relatively high tubercles (1–1.5 mm), while *O. cavernae* has more, but smaller ones (0.3–0.7 mm). *Oenothera harringtonii* has very distinctive large (2–3 mm high) tubercles, and *O. psammophila* and *O. caespitosa* subsp. *macroglottis* have odd wavy ridges rather than tubercles. The remaining taxa have such variable tubercles that they are not very useful in separating the taxa.

Seeds. Seed features have long been employed as a major consideration in the segregation of infrageneric groupings in *Oenothera* (cf. Spach, 1835a, 1835b; Raimann, 1893; Munz, 1965). In fact, Munz's (1931b) basic argument for including *O. primiveris, O. tubifera,* and *O. xylocarpa* in the same subgenus with *O. caespitosa* was their common possession of a seed-collar (raphial groove of Munz). In his summary work on Onagraceae for "North American Flora" Munz (1965) distinguished his subgenera of *Oenothera* largely on seed and capsule characters. Therefore, it was logical to examine critically the external and internal features of seeds in the *O. caespitosa* complex with the high resolving power of SEM in order to establish their utility in classification (Figs. 23–94).

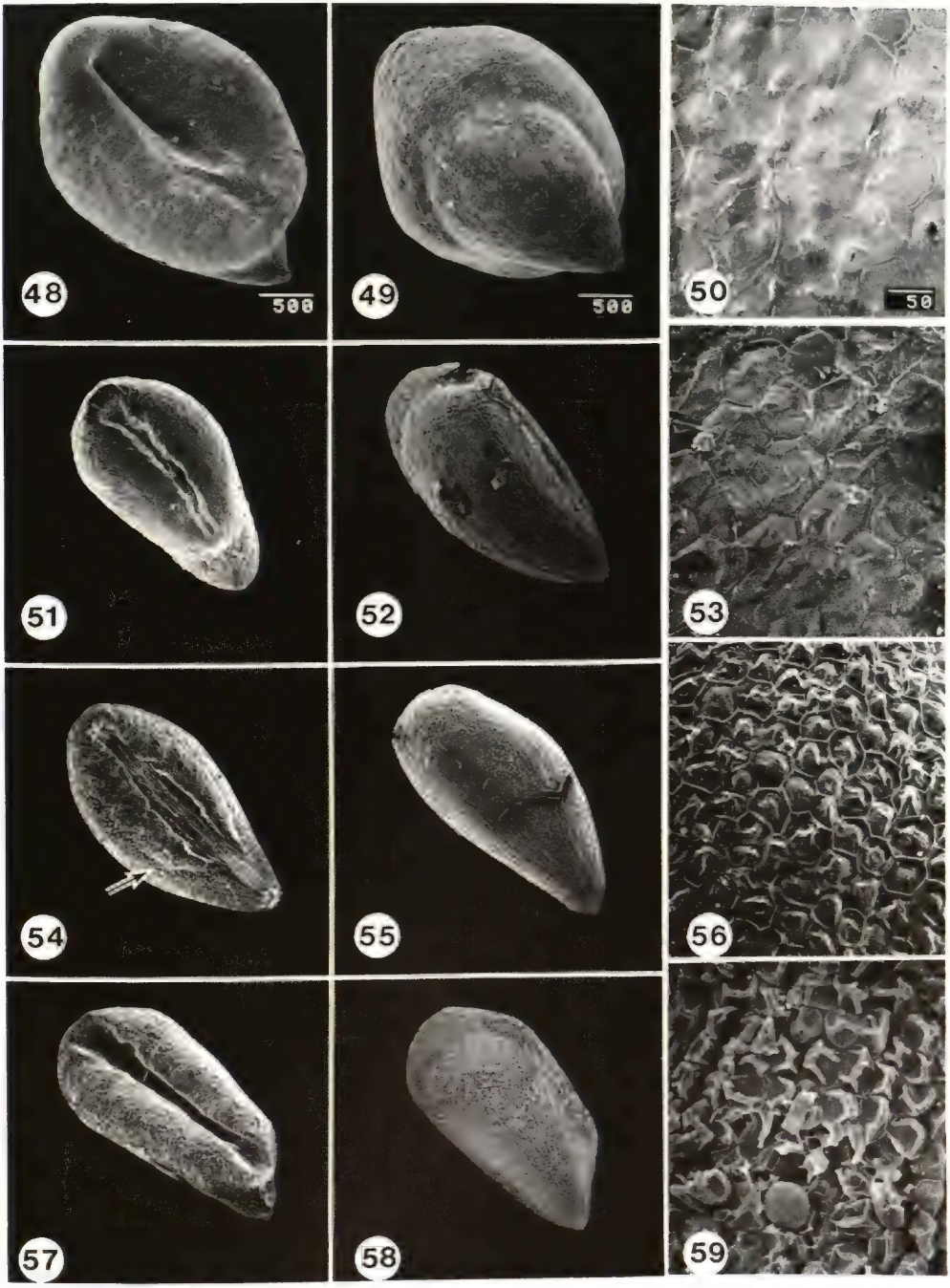
The seeds of the *Oenothera caespitosa* group are obovoid, or some minor modification of this basic shape. They are among the largest seeds in the genus, ranging from 2–3.5 mm long. Colors range from brown to dark reddish brown appearing black. The typically hollow chamber produced on the adaxial side of the seed (e.g., Fig. 85), along with the distinctive capsule morphology, clearly, set the *O. caespitosa* group apart from the rest of the genus. This chamber, referred to here as the seed-collar, is produced through a separation between two cell layers of the seed coat that forms during the course of development. Directly above the raphial ridge the collar is only one cell layer thick and appears as a thin translucent membrane. It can be observed clearly in Figures 85 (at the arrow) and 92. It appears that this seed-collar retains water that is of critical importance for germination and establishment in arid habitats with erratic rainfall such as those occupied by the *O. caespitosa* group. Evidence in support of this idea is found in the fact that when living seeds were placed on moistened filter paper the seed-collars imbibed water within a few hours, probably through the membrane. More importantly, the collars retained water for days after the filter paper had dried. This large hollow type of seed-collar is unique to the *O. caespitosa* complex, although the members of subg. *Pachylophus* sensu lato—including *O. primiveris, O. xylocarpa,* and *O. muelleri,* as well as some members of sects. *Oenothera, Lavauxia,* and *Megapterium*—have a small distal cavity that is clearly homologous with the seed-collar of the *O. caespitosa* group. The surface of the seeds of the *O. caespitosa* complex varies from papillose to reticulate or has an odd roughened appearance in which the surface cells are not externally visible. The size, shape, and features of the surface and collars present taxonomically meaningful patterns of variation among the taxa. Each is discussed below, along with comparisons with the patterns found in the other four species included by Munz (1931b, 1965) and



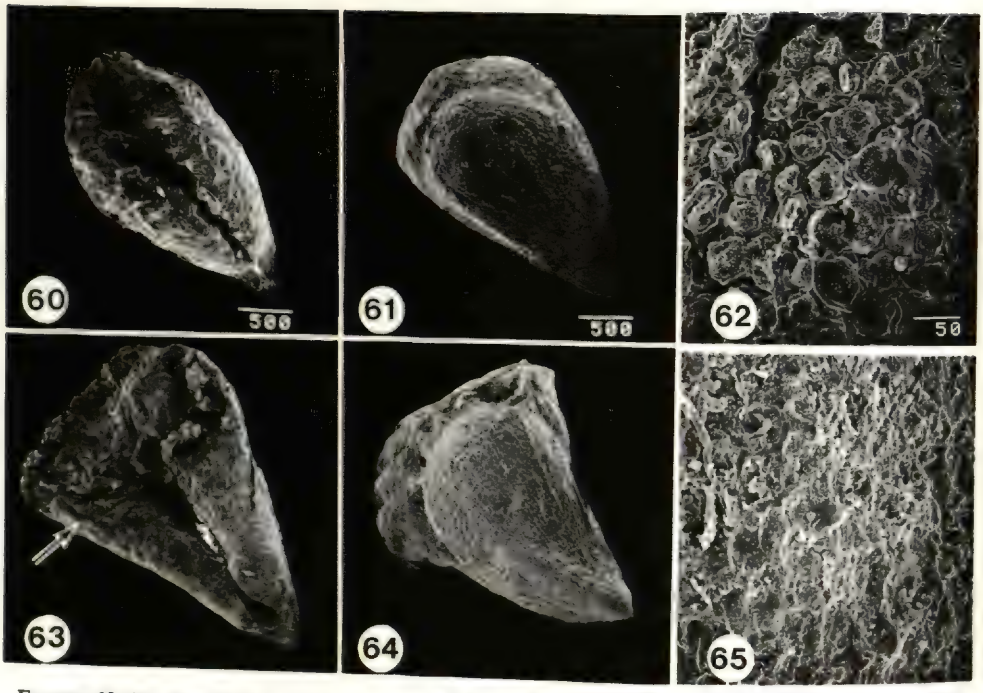
FIGURES 23–34. Scanning electron micrographs of seeds of *Oenothera caespitosa* subsp. *crinita*. The views are, left to right, adaxial followed by two abaxial views. Units of the scales are μm. The arrow in Figure 24 indicates the position of the distal end of the embryo. The smooth feature in the lower left of Figure 23 is glue contamination.



FIGURES 35–47. Scanning electron micrographs of seeds of *Oenothera caespitosa*.—35–40. subsp. *caespitosa*.—41–44. subsp. *navajoensis*.—45–47. subsp. *macroglottis*. The views are, left to right, adaxial followed by two abaxial views. Units of the scales are μm.



FIGURES 48–59. Scanning electron micrographs of seeds of species of the *Oenothera caespitosa* group.—48–53. *O. caespitosa* subsp. *marginata*.—54–56. *O. psammophila*.—57–59. *O. harringtonii*. The views are, left to right, adaxial followed by two abaxial views. Units of the scales are μm. The arrow in Figure 54 indicates the vestigial collar of *O. psammophila*.



FIGURES 60–65. Scanning electron micrographs of seeds of species of the *Oenothera caespitosa* group.—60–62. *O. cavernae.*—63–65. *O. brandegeei.* The views are, left to right, adaxial followed by two abaxial views. Units of the scales are μm. The arrow in Figure 63 indicates the margin of the collar of *O. brandegeei* which is opened and spread outward distally. The seed in Figure 63 has also been crushed, revealing the large internal cells.

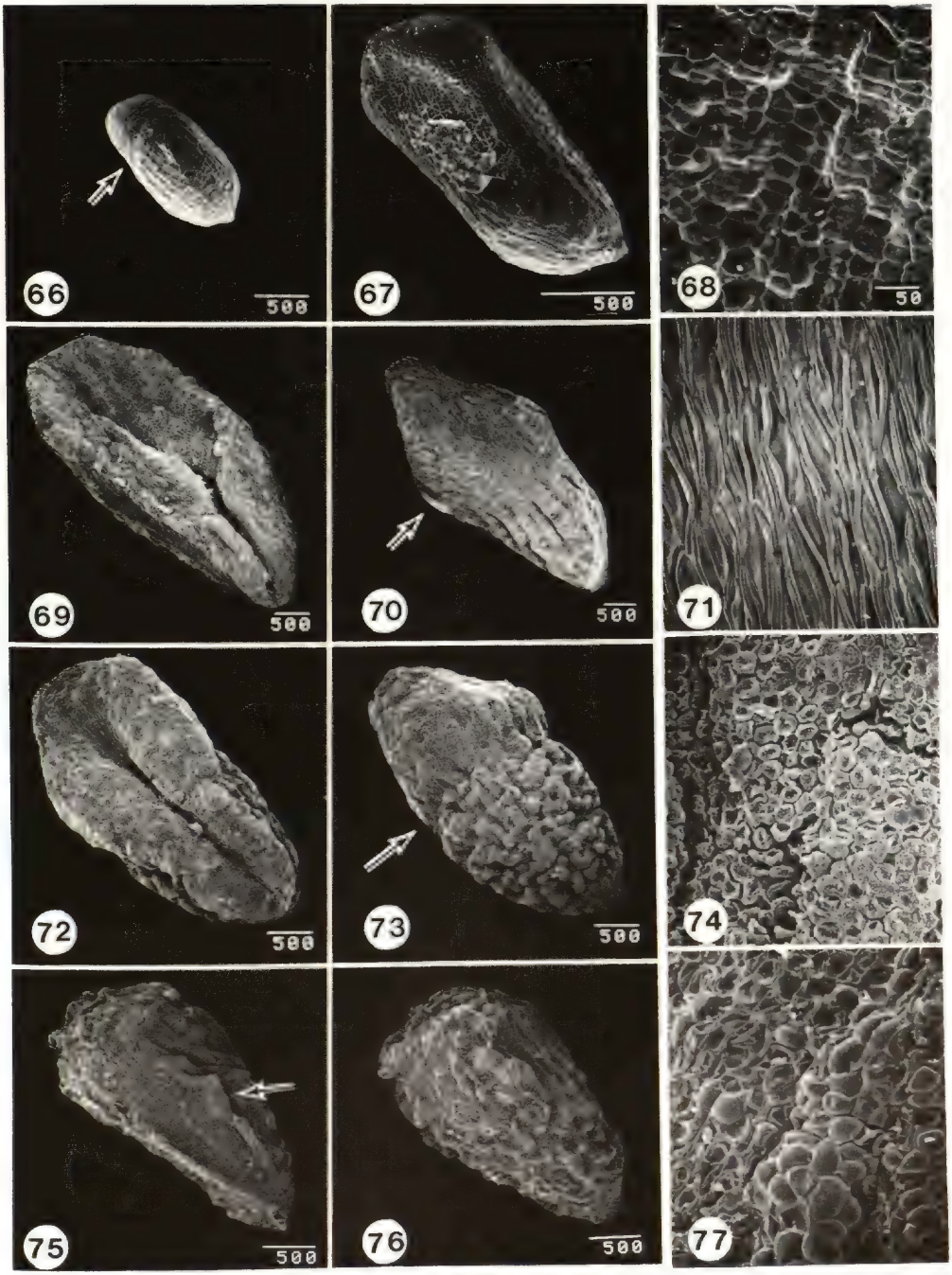
Raven (1970) in subg. *Pachylophus.* Seed features are summarized in Tables 4 and 5.

(1) *Number of rows per locule*—the *Oenothera caespitosa* group, in general, is characterized by fruits with two adjacent and distinct rows of seeds per locule. Sometimes these two rows are partially overlapping. This crowding causes the seeds to be positioned in the capsule with the raphe at various angles relative to the capsular axis. Crowding is caused by either larger embryos (*O. caespitosa* subsp. *caespitosa*) or more commonly larger collars (*O. caespitosa* subsp. *crinita,* Figs. 29, 30; subsp. *marginata,* Figs. 48, 49, 85; and *O. brandegeei,* Figs. 63, 64). Less commonly extreme crowding leads to the disposition of the seeds in one irregular row per locule and a concomitant decrease in total number of seeds per capsule, such as in some plants of *O. caespitosa* subsp. *marginata,* which have greatly inflated collars, from Arizona (Figs. 48, 49, 85). A similar pattern is found in the four species related to the *O. caespitosa* group. The seeds of *O. macrosceles, O. primiveris,* and *O. xylocarpa* are also arranged in two adjacent rows while the large seeds of *O. muelleri* are arranged in a single row.

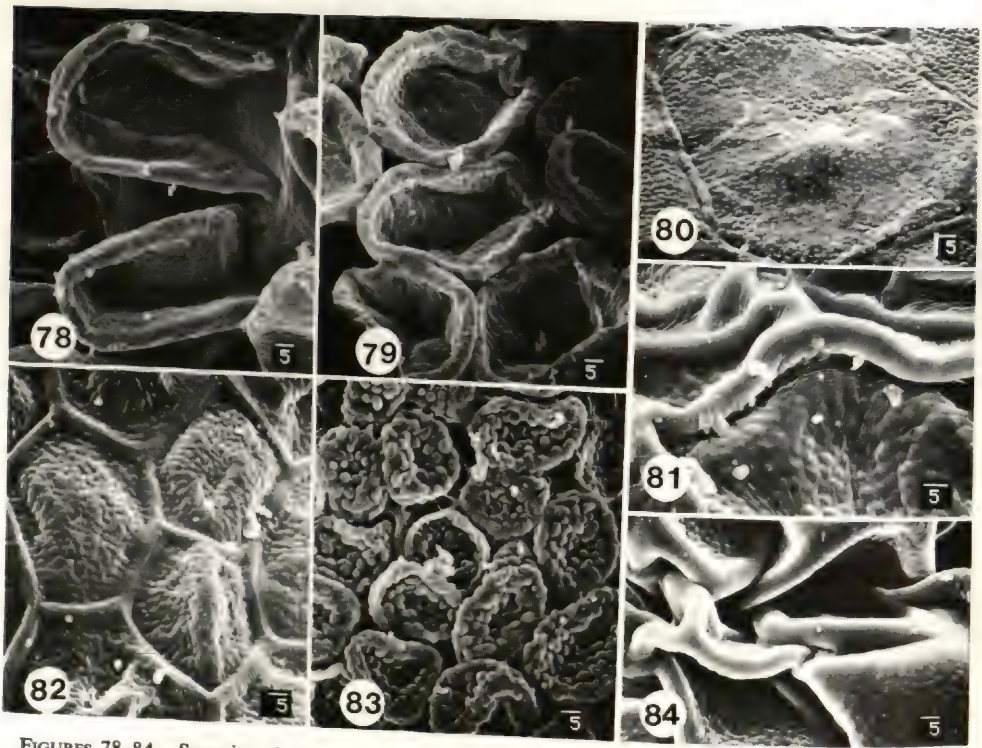
(2) *Shape*—the basic seed shape is obovoid, although this, through modifications of the collar, may be altered to nearly orbicular (Figs. 48, 49), or triangular (Figs. 29, 30, 63, 64). Sometimes the seeds are somewhat curved (e.g., Fig. 64). Ellipsoid seeds do not occur in the *Oenothera caespitosa* group, but are common in sect. *Oenothera,* represented here by *O. macrosceles* (Figs. 66, 67).

(3) *Surfaces*—features of the seed coat surface can be divided into three hierarchical categories: (a) "surface topography" refers to gross variations in the total aspect of the seed resulting from differential thickness of the seed coat or convolutions of groups of cells; (b) "surface sculpture" includes those variations that specifically relate to the conformation of the exposed periclinal wall of the surface cells; and (c) "microsculpture" refers to the features of the surface of each cell.

The seeds of the *Oenothera caespitosa* group have remarkably little gross surface topography.



FIGURES 66–77. Scanning electron micrographs of seeds of species related to the *Oenothera caespitosa* species group.—66–68. *O. macrosceles.*—69–71. *O. muelleri.*—72–74. *O. primiveris.*—75–77. *O. xylocarpa.* The views are: Figure 66, abaxial; Figure 67, lateral; all others are, left to right, adaxial followed by two abaxial views. Units of the scales are μm. The arrows in Figures 66, 70, and 73 indicate the position of the distal end of the embryo, whereas in Figure 75 the arrow indicates one of the two longitudinal ridges that appears to be a vestigial collar.

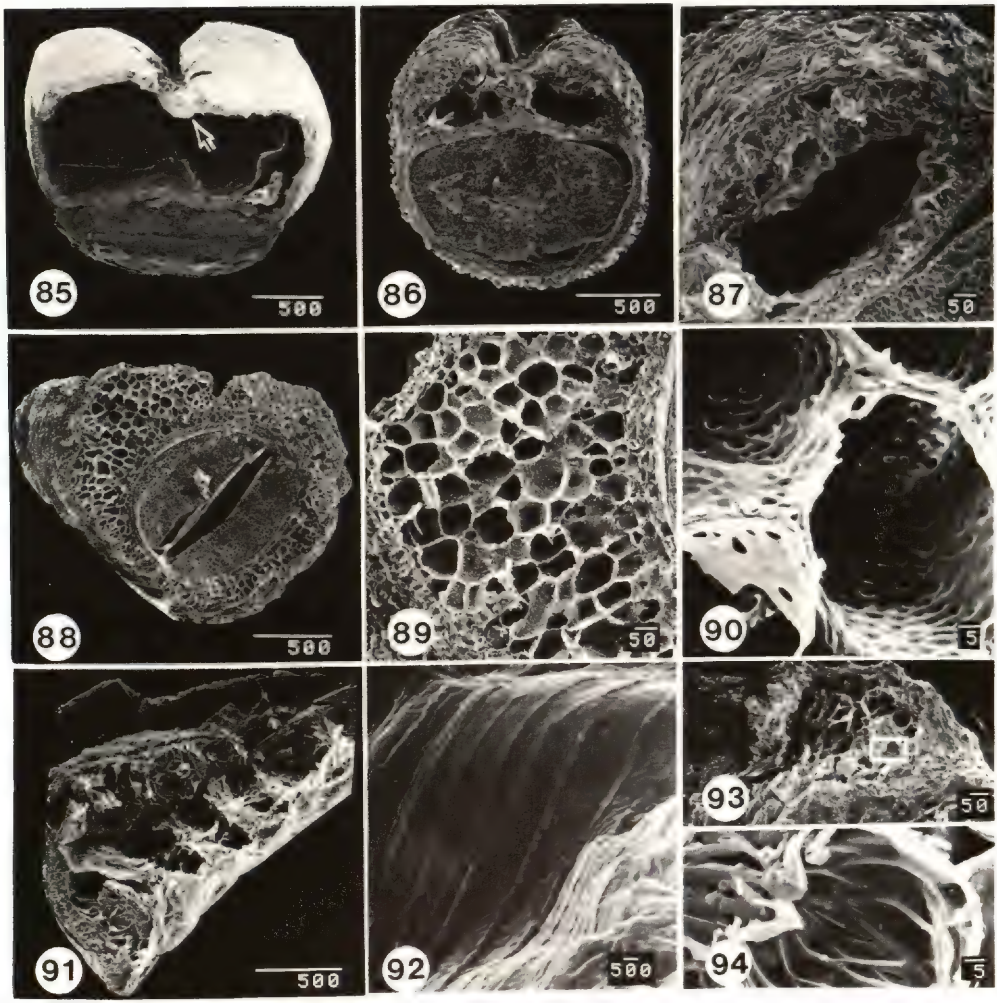


FIGURES 78–84. Scanning electron micrographs of abaxial surfaces of seeds of the *Oenothera caespitosa* group, *O. primiveris* and *O. xylocarpa*.—78, 79. *O. caespitosa* subsp. *caespitosa*.—80. subsp. *marginata*.—81. subsp. *macroglottis*.—82. *O. psammophila*.—83. *O. primiveris*.—84. *O. xylocarpa*. Units of the scales are μm.

In contrast, the seeds of *O. primiveris* (Fig. 73) and *O. xylocarpa* (Fig. 76) are coarsely rugose on the adaxial surface at the proximal end of the seed which contains the embryo. *Oenothera muelleri* (Fig. 70) has, in the same position, coarse longitudinal ridges, whereas *O. macrosceles* (Fig. 66) has a less conspicuous pitted surface. These topographic features are largely the result of a differential number of cell layers in the testa. In *O. xylocarpa*, however, the ridges are partly formed by groups of turgid papillae adjacent to collapsed papillae (Fig. 77). Thus the principal parts of the seed with obvious surface topography in this group of *Oenothera* species are those containing the embryo.

Surface sculpture provides useful taxonomic characters in spite of the fact that the different types of surface sculpture appear to be relatively minor genetic variations on a common theme. The exposed periclinal cell walls of the seed surface in the *Oenothera caespitosa* group are typically strongly convex, forming a distinctive papillose surface. The papillae may be laterally collapsed, as in some individuals of *O. caespitosa* (Figs. 30, 31, 33–43, 78, 79), mostly turgid (Figs. 46, 47), or a combination of collapsed and turgid (Figs. 58, 59). The seed-collars of papillose seeds, however, generally have completely collapsed papillae that appear as reticulations (Figs. 29, 32, 35, 38, 41, 45, 57, 81). This condition presumably results from the greater enlargement of the individual cells of the collar relative to those from the embryo portion. Similarly collapsed and flattened papillae also occur as small patches at various locations over the seed surface. In this case the flattening is produced by pressure during development from adjacent seeds and/or the ovary wall (e.g., Fig. 30, lateral and distal part of abaxial faces).

The three species most closely allied to the *Oenothera caespitosa* complex also have seeds with papillose surfaces although in the case of *O. muelleri* they are greatly modified. *Oenothera xylocarpa* has a combination of turgid and collapsed papillae (Figs. 77, 84). The turgid papillae contribute to the ridges on the coarsely rugose



FIGURES 85–94. Scanning electron micrographs of seeds of the *Oenothera caespitosa* species group and *O. primiveris*.—85. *O. caespitosa* subsp. *marginata*, cross-section.—86, 87. subsp. *caespitosa*, cross-section.—88–90. *O. primiveris*, cross-section.—91. *O. caespitosa* subsp. *crinita*, internal view of the length of the seed-collar.—92. subsp. *navajoensis*, seed-collar membrane.—93, 94. *O. brandegeei*, distal end of seed-collar showing large cells inside collar with thickenings. The arrow in Figure 85 indicates the membrane of *O. caespitosa* subsp. *marginata*. Units of the scales are μm.

surface topography while the collapsed papillae comprise the valleys. *Oenothera primiveris* has densely crowded papillae that are usually depressed apically (Figs. 74, 83). These modifications greatly increase surface area and presumably aid in a greater ability to adsorb water or dissipate heat in this Sonoran Desert annual. Finally, *O. muelleri* has flattened papillae on the adaxial surface that appear as rather isodiametric reticulations and extremely longitudinally elongated papillae on the abaxial surface (Figs. 70, 71). These distortions appear to be directly related to the great size (up to 6–7 mm long) of the seeds.

Another type of surface sculpture presumably derived from the papillose type is a reticulate surface (e.g., Fig. 80). This type, where it occurs, is uniform throughout the seed. It is known consistently in all populations of *Oenothera caespitosa* subsp. *marginata* (Figs. 48–53) and of *O. cavernae* (Figs. 60–62) thus far examined, but also occurs sporadically in some populations of

TABLE 4. Comparison of seed characters of the *Oenothera caespitosa* group and four closely related species.

Species	Number of Rows per Locule	Shape	Abaxial Surface Features		
			Topography (Embryo Portion)	Sculpturing	Microsculpturing
O. caespitosa					
Subsp. *crinita*	2	Obovoid, oblong, or roughly triangular	No relief	Collapsed papillose, reticulate, or roughened	Conspicuous or inconspicuous micropapillae
Subsp. *caespitosa*	2 rarely, 1 irregular	Narrowly obovoid	No relief	Collapsed papillose	Inconspicuous micropapillae
Subsp. *navajoensis*	2	Narrowly obovoid	No relief	Collapsed papillose or reticulate	Inconspicuous to conspicuous micropapillae
Subsp. *macroglottis*	2	Obovoid	No relief	Turgid to somewhat collapsed papillose	Conspicuous micropapillae
Subsp. *marginata*	2 overlapping, rarely only 1 irregular	Obovoid to nearly orbicular	No relief	Reticulate	Conspicuous micropapillae
O. psammophila	2	Narrowly obovoid	No relief	Pustulate-reticulate	Conspicuous micropapillae
O. harringtonii	2	Narrowly obovoid	No relief	Collapsed papillose with some turgid papillae	Conspicuous micropapillae
O. cavernae	2	Obovoid	No relief	Reticulate or collapsed papillose	Conspicuous micropapillae
O. brandegeei	2 partially overlapping	Irregularly triangular	No relief	Roughened	Inconspicuous micropapillae
O. macrosceles	2	Oblong-ellipsoid	Pitted	Reticulate	Smooth
O. muelleri sensu lato	1	Obovoid to fusiform	Longitudinally ribbed	Collapsed papillose or with elongated papillae	Conspicuous micropapillae
O. primiveris	2	Obovoid	Coarsely rugose	Apically depressed papillae	Very large micropapillae
O. xylocarpa	2	Obovoid	Coarsely rugose	Turgid and collapsed papillae	Conspicuous micropapillae

O. caespitosa subsp. *navajoensis* (Fig. 44) and subsp. *crinita* (Figs. 26–28). Based on other evidence presented later, it appears that reticulate surfaces have either evolved independently on several occasions or, less likely, were obtained by some populations taxonomically assigned to subsp. *navajoensis* and subsp. *crinita* on the basis of their overall characteristics via hybridization

TABLE 5. Comparison of seed-collar characters of the *Oenothera caespitosa* group and four closely related species. NA = not applicable.

Species	Embryo Portion	Seed-collar Type	Margin	Membrane at Maturity	Internal Ribbing
O. caespitosa					
Subsp. *crinita*	⅓–½	*O. caespitosa*	Distally sinuate or sinuate throughout	Depressed, splitting	Yes
Subsp. *caespitosa*	½–⅔	*O. caespitosa*	Distally sinuate	Depressed, splitting	Yes
Subsp. *navajoensis*	½	*O. caespitosa*	Distally sinuate or entire	Broad, undulate, not splitting	No
Subsp. *macroglottis*	ca. ½	*O. caespitosa*	Entire	Narrow, not splitting	No
Subsp. *marginata*	⅓–½	*O. caespitosa*	Distally sinuate or entire	Narrow, not splitting	No
O. psammophila	⅞	*O. caespitosa*	Distally sinuate	Broad, not splitting	Yes (?)
O. harringtonii	½	*O. caespitosa*	Distally sinuate	Depressed, not splitting	No
O. cavernae	ca. ½	*O. caespitosa*	Sinuate throughout	Absent	Yes
O. macrosceles	1	Distal cavity	NA	NA	NA
O. muelleri sensu lato	½	*O. primiveris*	NA	NA	NA
O. primiveris	⅓–½	*O. primiveris*	NA	NA	NA
O. xylocarpa	1	Vestigial (?)	NA	NA	NA

with subsp. *marginata*. The seeds of *O. psammophila* are unique in having small irregularly raised pustules within most of their surface reticulations (Figs. 55, 56, 82). At the juncture of the collar and the embryo portion of the seeds of *O. psammophila*, however, there are more typical papillae (Fig. 54, at the arrow). The characteristics of the surface of the seeds of *O. psammophila* support the idea of a hybrid origin of this species from *O. caespitosa* subspp. *marginata* and *caespitosa*. *Oenothera macrosceles* (Figs. 66–68), like many other species of sect. *Oenothera* (cf. Dietrich, 1977), has a reticulate surface that is rather different in appearance from those of any members of the *O. caespitosa* group.

The third type of surface sculpture in seeds of the *Oenothera caespitosa* complex is a rather amorphous roughened surface in which individual cells are not conspicuous. It is known only in *O. brandegeei* (Figs. 63–65) and high-elevation populations of *O. caespitosa* subsp. *crinita* (Figs. 23–25). The roughened surface type is perhaps nothing more than an extreme reduction of the papillose type, and may have evolved independently in each of these taxa.

The microsculpturing of the cells, although somewhat variable, is not particularly useful in separating any of the taxa studied here. It may, however, be of more utility in making broader comparisons within the genus. Cells of *Oenothera macrosceles* (sect. *Oenothera*) have a smooth surface at 250× (Fig. 68), whereas all of the other taxa studied have minute micropapillae. Based on size, the micropapillae can be divided into three groups. Some taxa have rather inconspicuous micropapillae. This surface correlates well with lateral-collapsed papillose and irregular roughened surfaces (Figs. 25, 31, 37, 40, 43, 64). Most of the taxa have distinctive micropapillae (Figs. 28, 34, 47, 50, 53, 56, 59, 62, 71, 77, 80, 82, 84). Only *O. primiveris* has large very striking micropapillae (Figs. 74, 83), which may represent another mechanism to increase the seed surface to volume ratio for water adsorption or heat dissipation in an extremely xeric environment.

(4) *Collar types*—the seeds of the *Oenothera caespitosa* group and other related species studied here have two basic types of seed-collars: one in the *O. primiveris* and *O. muelleri* and the other in the *O. caespitosa* complex. A third, and presumably more generalized, type of structure is a

distal cavity, the taxonomic distribution of which is in need of study, but is presently known to occur in sect. *Oenothera* subsects. *Emersonia*, *Raimannia*, and *Munzia*, sect. *Kleinia*, and sect. *Megapterium*. Both types of seed-collars probably originated through an enlargement of the distal cavity into the area of the raphe.

In those seeds with a distal cavity the chalazal end of the seed is composed of multicellular layers and constitutes 15–20% of the total seed length. The constituent cells are large relative to other cell layers of the testa. When cross-sectioned, a small cavity is exposed. This cavity extends for a short distance beneath the surface layers on the raphial face. The external features of this structure are shown in Figure 66 at the arrow. In species with a distal cavity, such as *Oenothera macrosceles*, the raphial face, shown to the right side in lateral view in Figure 67, has more cell layers than the abaxial surface (to the left in Fig. 67), but otherwise has no special external or internal features other than the extension of the cavity into the area.

By contrast, seeds with the collar of *Oenothera primiveris* have a much larger multicellular region at the chalazal end that often constitutes over 30–45% of the total seed length (Fig. 73, at the arrow). The enclosed cavity is, likewise, considerably larger. In addition to these modifications the regions on either side of the raphe are multicellular (Figs. 88, 89). This creates a striking raphial groove (Fig. 72), which is homologous to those in the *O. caespitosa* group. The constituent cells of the raphial edges are greatly enlarged isodiametric cells with very distinctive pitting (Fig. 90). There is a unicellar membrane depressed in the raphial groove, but it typically disintegrates before the seed reaches maturity. *Oenothera muelleri* has features very similar to those described for the seed-collar of *O. primiveris* (Figs. 69, 70). In some seeds of *O. muelleri* from Nuevo Leon not illustrated here, the raphial groove is not at all visible externally since it has several layers of the large cells above it. Thus the groove is transformed into a slender hollow tube traversing the raphial face of the seed that connects to a distal cavity like that found in the seeds of *O. primiveris*.

The seed coat of *Oenothera xylocarpa* is very unusual. It lacks both the multicellular chalazal structure and a seed-collar. The raphial face, however, does possess two longitudinal ridges on either side of the inconspicuous raphe (Fig. 75, at arrow). These ridges are presumably a vestigial seed-collar.

The seed-collars of the *Oenothera caespitosa* group are the most specialized among those of the species discussed, and, as mentioned above, function to store water used in germination. These collars differ from those of other species in that there is no differentiation internally between the raphial groove region and the extended chalazal region. Further, the combined cavity is greatly enlarged (Figs. 85–87). The seeds of all of the taxa of the *O. caespitosa* complex have a unicellular membrane above the raphial ridge (Fig. 92), except for those of *O. cavernae* (Fig. 60) and those of some populations of *O. caespitosa* subsp. *crinita* (Fig. 26), in which the membrane is absent at maturity and the cavity is open. In *O. psammophila*, the entire collar is very reduced and flattened (Fig. 54). The seed-collar of *O. brandegeei* has the most distinctive specialization in the group: its distal margins are rolled outward (Fig. 63, margin of collar at arrow) and the entire cavity is filled with large cells (Figs. 93, 94). But, these are unlike the cells in the collar of *O. primiveris* (Figs. 89, 90), the collar-cells of *O. brandegeei* have thickenings and lack the perforations present in the cells of *O. primiveris*. Since *O. brandegeei* grows in the most xeric habitat of any taxon in the *O. caespitosa* group, it would not be surprising if these cells retain water more effectively than does an empty cavity.

Features of the seed-collar, especially internal ones, have been exceedingly useful in understanding relationships among the taxa. The following have been used both in determining relationships and detecting hybrids:

(a) *Collar margin*—it is entire to distally sinuate in most of the taxa (e.g., Figs. 35, 38, 41, 45) but conspicuously sinuate throughout in most seeds of *Oenothera caespitosa* subsp. *crinita* (Figs. 26, 29, 32), *O. cavernae* (Fig. 60), and *O. brandegeei* (Fig. 63, at the arrow).

(b) *Membrane*—in some taxa (Figs. 23, 29, 32, 35, 38) the membrane is depressed into the groove and usually splits at maturity, whereas it is broader, rarely depressed and usually remains intact at maturity in *Oenothera caespitosa* subsp. *navajoensis* (Fig. 41), subsp. *macroglottis* (Fig. 45), subsp. *marginata* (Figs. 48, 51), *O. psammophila* (Fig. 54), and *O. harringtonii* (Fig. 57).

(c) *Internal features*—in some taxa, such as *Oenothera caespitosa* subsp. *marginata*, the collar cells are smaller and densely compressed (Fig.

85), whereas in subsp. *caespitosa* they are larger (Figs. 86, 87). More diagnostic are the transverse ribs on the internal wall of the collar (e.g., Fig. 91), which are sometimes visible externally in *O. caespitosa* subsp. *crinita* (Fig. 29). Internal ribbing occurs in all taxa except *O. caespitosa* subspp. *marginata, navajoensis,* and *macroglottis,* and *O. harringtonii* which have relatively smooth internal walls (e.g., Fig. 85).

In summary, the *Oenothera caespitosa* species complex is quite distinctive morphologically. It is unique in *Oenothera* in its possession of obtusely angled capsules with tubercles or raised ridges along the margins of the valves and the seeds with a large internal cavity, and a seed-collar on the adaxial side of the seed. In addition, the combination of the lack of short, closely appressed pubescence, the possession of white petals and dark reddish brown seeds separate the species of the *O. caespitosa* group from the three species most closely related to them.

Features of most organs of the plant body are useful to some degree in distinguishing taxa within the *Oenothera caespitosa* group. Characters of the stem, root, leaves, and flowers although, at least, modally distinctive in each taxon, are so variable within the taxa or even on one individual as to be difficult to utilize taxonomically. In contrast, pubescence type, capsule and seed morphology provide an excellent array of characters that not only distinguish the taxa from one another, but are useful in the detection of hybrids (see p. 39) and in the study of the phylogeny of the group (see p. 45).

Cytology and Artificial Hybridization

From 1969 to 1972 an extensive greenhouse program was carried out by Stockhouse (1973) to investigate the crossing relationships and to determine chromosome numbers and meiotic configurations of wild strains as well as hybrids. This investigation was extended by Wagner during 1979–1981, primarily to include *Oenothera cavernae,* so that now all nine of the taxa in the complex have been involved in the program. The experimental greenhouse program was initiated to investigate the existence of internal crossing barriers and to study the role of chromosomal repatterning or genomic differentiation in the diversification of these taxa. Morphological study of the artificial hybrids has also been useful in aiding in the detection of putative natural hybrids discussed in the next section.

Cytology

Cytological observations were made from buds collected in the field or more often from greenhouse-grown progeny from wild-collected seed. A total of 66 strains representing all nine taxa were examined (Table 6), including 12 earlier records (Bills, 1968; Gregory & Klein, 1960; Kurabayashi et al., 1962; Stockhouse, 1976).

Buds for meiotic chromosome studies were collected from three to five individuals per population, fixed in 1 : 3 acetic acid : absolute ethanol for 3–24 hr. and stored in 70% ethanol under refrigeration. Prior to staining, the buds were hydrolyzed in a 1 : 1 mixture of concentrated HCl and 95% ethanol for 8–11 min. (Lewis & Lewis, 1955). The anthers were squashed in acetocarmine, and the slides were made permanent by the addition of Hoyer's mounting medium following the procedure described by Beeks (1955). Subsequent observations were made with a Zeiss Standard WL microscope with phase contrast or a Zeiss Photomicroscope II equipped for Nomarski differential interference contrast. Meiotic configurations were documented with camera lucida drawings or photomicrographs.

All plants examined were diploid, $n = 7$, or tetraploid, $n = 14$. *Oenothera,* all species of which are known cytologically, has a basic chromosome number of $x = 7$, with no aneuploidy known. Polyploidy occurs sporadically in several sections of the genus, ranging from none in the 76 species of sect. *Oenothera,* to intraspecific polyploidy as in some populations of *Oenothera coronopifolia* Torrey & A. Gray in sect. *Kleinia* (Gregory & Klein, 1960), or species in which all populations are polyploid, as in two of the five species in sect. *Kneiffia* (Straley, 1977). The *Oenothera caespitosa* group, as indicated in Table 7, falls into the intermediate category, having sporadic intraspecific polyploidy. Nine collections or 14% of the total sampled were tetraploid. The tetraploids were morphologically indistinguishable in all cases from adjacent diploids and therefore were presumably consistently derived from them. They formed at least some quadrivalents. Tetraploid populations were found in three of the subspecies of *O. caespitosa.* In *O. caespitosa* subspp. *crinita* and *navajoensis,* with one tetraploid plant each, polyploidy appears to be of sporadic occurrence in otherwise diploid populations. Additional plants grown by Stockhouse from the same population of *O. caespitosa* subsp. *crinita* that gave the single tetraploid count (*Wiens s.n.,* Inyo County, California) were all

TABLE 6. Chromosome observations of plants in the *Oenothera caespitosa* group.

Species	Locality and Collector[a,b]	Source[b]	Chromosome Observations[c]
Oenothera caespitosa			
Subsp. *caespitosa*	Montana		
	Broadwater Co.		
	*S 131**	Stockhouse, 1976, (as subsp. *purpurea*)	5_{II} + ch 4
	Wyoming		
	Fremont Co.		
	S 143	Stockhouse, 1976	7_{II}
	Lincoln Co.		
	S 128	S	7_{II}
	Teton Co.		
	*S 133**	Stockhouse, 1976	7_{II}
Subsp. *crinita*	California		
	Inyo Co.		
	E of Independence		
	D. Weins s.n.	S	7_{II}
	E of Independence		
	D. Weins s.n.	G	$5_{IV} + 4_{II}$
	Without locality		
	*K 2654**	S	7_{II}
Subsp. *macroglottis*	Colorado		
	Boulder Co.		
	G 20	S	7_{II}
	S 120	S	7_{II}
	S 123	S	7_{II}
	El Paso Co.		
	S 115	S	$n = 14$
	S 116	S	$4_{IV} + 6_{II}$
	Gold Camp Rd.		
	S 117	S	$3_{IV} + 8_{II}$
	S 118	S	$n = 14$
	Gunnison Co.		
	1 mi. N of Almont		
	K 1968	G	7_{II}
	Jackson Co.		
	2.2 mi. NE Big Creek Lakes		
	K 2185	G	7_{II}
	Larimer Co.		
	5 mi. W of mouth of Rist Canyon		
	G 21	G	7_{II}
	3.1 mi. W of Bellvue		
	S 105	S	7_{II}
	Horsetooth Reservoir		
	S 109	S	7_{II}
	S 114	S	7_{II}
	S 119	S	7_{II}
	*S 121**	Stockhouse, 1976 (as subsp. *montana*)	7_{II}

TABLE 6. (Continued).

Species	Locality and Collector[a,b]	Source[b]	Chromosome Observations[c]
	Routt Co.		
	2.4 mi. W of Oak Creek		
	K 1735	G	7_{II}
	Trout Creek, N of Oak Creek		
	K s.n.	S	7_{II}
	Saguache Co.		
	G 11	G	$n = 14$
	Summit Co.		
	Green Mt.		
	K s.n.	S	$n = 14$
	Teller Co.		
	S 110	S	$n = 14$
	Utah		
	San Juan Co.		
	S 537	S	7_{II}
Subsp. *marginata*	Arizona		
	Coconino Co.		
	Page		
	Anderson s.n.	S	7_{II}
	California		
	Inyo Co.		
	Gregory 392	K	7_{II}
	Mono Co.		
	K 416	Gregory & Klein, 1960	5_{II} + ch 4
	San Bernardino Co.		
	Gregory 374	K	7_{II}
	Wolf 9532	G	7_{II}
	Idaho		
	Bannock Co.		
	S 553	S	$n = 7$
	Fremont Co.		
	*S 238**	S	7_{II}
	Nez Perce Co.		
	N of Lewiston		
	1961, *Bills s.n.*	Bills, 1968	5_{II} + ⊙4
	Nevada		
	Clark Co.		
	Gregory 385	K	7_{II}
	Eureka Co.		
	Raven 15416	Kurabayashi et al., 1962	$2n = 14$
	Mineral Co.		
	Lake Walker		
	Raven s.n.	G	7_{II}
	Nye Co.		
	*K 2612**	S	5_{II} + ⊙4
	K 2642	S	5_{II} + ⊙4
	New Mexico		
	McKinley Co.		
	Mollica 27	S	7_{II}

TABLE 6. (Continued).

Species	Locality and Collector[a,b]	Source[b]	Chromosome Observations[c]
	Sandoval Co.		
	*K 1479**	G, S	7_{II}
	W et al. 4401	W	$5_{II} + \odot 4$
	Utah		
	Cache Co.		
	1960, *Shaw s.n.*	K	7_{II}
	Grand Co.		
	14 mi. E of Cisco		
	*S 214**	S	7_{II}
	Wyoming		
	Lincoln Co.		
	S 127	Stockhouse, 1976	7_{II}
Subsp. *navajoensis*	Utah		
	Grand Co.		
	Colorado River Canyon across salt wash		
	S 215	Stockhouse, 1976 (as subsp. *jonesii*)	7_{II}
	*S 216**	S	7_{II}
	*S 532**	S	7_{II}
	*S 534**	S	7_{II}
	San Juan Co.		
	*S 547**	S	14_{II}, 1_{I}^{+} 7_{II} + 2_{I}^{+} 1_{V}
	*S 549**	S	7_{II}
Oenothera brandegeei	Baja California		
	*Moran 12983**	Stockhouse, 1976	7_{II}
Oenothera cavernae	Nevada		
	Clark Co.		
	*W 3994**	W	7_{II}
	*W 3998**	W	7_{II}
	*W 3999**	W	$n = 7$
	W 4595	W	7_{II}
Oenothera harringtonii	Colorado		
	El Paso Co.		
	S 111	S	7_{II}
	S 137	S	7_{II}
	Fremont Co.		
	1 mi. S of Florence		
	G 18	G	7_{II}
	S 112	S	7_{II}
	*S 113**	Stockhouse, 1976 (as *O. eximia*)	7_{II}
Oenothera psammophila	Idaho		
	Fremont Co.		
	*S 247**	Stockhouse, 1976	7_{II}
	1 mi. N Parker		
	*S 521a**	S	7_{II}
	1 mi. N Parker		
	2 mi. NW		
	S 521b	S	7_{II}

TABLE 6. (Continued).

Species	Locality and Collector[a,b]	Source[b]	Chromosome Observations[c]
	1 mi. N Parker 1 mi. NW		
	S 521c	S	7_{II}

[a] Locality information for the chromosome count is given in the systematic treatment unless there is no voucher, then the locality is reported in this table. The asterisk after a collection indicates a strain that was used in the artificial crossing program.

[b] S = Robert Stockhouse in Stockhouse, 1973; G = Raylene Goeken in Goeken, 1968; K = William M. Klein; W = Warren L. Wagner.

[c] ⊙ = ring or ch = chain at meiotic metaphase I or diakinesis, II = bivalent, I = univalent, IV = quadrivalent, V = pentavalent.

diploid. The one tetraploid of *O. caespitosa* subsp. *navajoensis* had 25% stainable pollen, while all other tetraploids studied had pollen stainability over 90%. This one tetraploid plant was from Lake Powell, San Juan County, Utah (*Stockhouse 547*). Another collection, *Stockhouse 549*, from the same general area was diploid. In contrast, seven collections (35%) of *O. caespitosa* subsp. *macroglottis* were tetraploid. These collections all were made in the east-central portion of the range of this subspecies. Four of the seven tetraploid determinations were from a transect along the road to Pikes Peak in El Paso County, Colorado. No diploid plants are known from this area. A fifth tetraploid individual was from adjacent Teller County; the remaining two were from the widely separated counties of Summit and Saguache. More material should be studied from the intervening areas to determine whether all of the plants in the area delimited by these three regions are tetraploid. In any event, it appears that polyploidy has played only a minor role in the evolution of the group.

Polyploidy does not interfere with the functioning of the self-incompatibility system and all tetraploid populations were self-incompatible. This, in fact, is the consistent pattern throughout the Onagraceae. There are ten genera that include self-incompatible species and five of these have some species or populations that are self-incompatible polyploids (Raven, 1979).

Translocation heterozygosity is not common in the group. Only six plants from different populations or 10% of the diploid total were heterozygous for one reciprocal translocation (5_{II} + ⊙4) and no individuals were found that were heterozygous for more than one. As with polyploidy, all translocations were found in *O. caespitosa*: one in subsp. *caespitosa* and the other five in subsp. *marginata*. The distribution of single translocations in *O. caespitosa* subsp. *marginata* suggests that they occur sporadically throughout its geographical range. The widespread occurrence of reciprocal translocations in natural populations is a characteristic feature of all genera of the tribe Onagreae (Raven, 1979).

ARTIFICIAL HYBRIDIZATION

Strains used in the crossing program are indicated in Table 6. Meiotic configurations and pollen stainability were determined by the methods discussed in the preceding section. *Oenothera cavernae* and *O. brandegeei* are the only self-compatible species in the group, and must be carefully emasculated prior to pollen transfer by hand. After pollination, the plants were isolated in insect-proof cages until their flowers withered. Self-incompatibility of each strain used in the crossing program was determined by repeated selfing; the results are reported in Table 6, along with those plants determined from natural populations. Altogether more than 1,100 crosses were made, including 255 interspecific crosses in most combinations among the species of the *O. caespitosa* complex, 740 crosses among the five subspecies of *O. caespitosa*, and 113 crosses between the taxa of the *O. caespitosa* complex and those species that on morphological grounds appear to be most closely related.

Hybrids are relatively easily obtained among the subspecies of *Oenothera caespitosa*. When especially long-styled plants (such as those of *O. caespitosa* subsp. *marginata*) are used as the pistillate parent, pollen from a shorter-styled plant may not be able to grow down the entire length of the long style. Consequently such a cross can sometimes be made only if the individual with

TABLE 7. Frequency of meiotic configurations and tetraploidy in natural populations.

Species	Number of Populations Sampled	Number of Diploid Populations with Various Meiotic Configurations		Number of Tetraploid Individuals
		7_{II}	$5_{II} + \odot 4$	
Oenothera caespitosa	50	37	6	9
Subsp. *caespitosa*	4	3	1	0
Subsp. *crinita*	2	2	0	1[a]
Subsp. *macroglottis*	21	14	0	7
Subsp. *marginata*	18	13	5	0
Subsp. *navajoensis*	6	5	0	1
Oenothera brandegeei	1	1	0	0
Oenothera cavernae	3	2	0	0
Oenothera harringtonii	5	5	0	0
Oenothera psammophila	4	4	0	0
Totals	64	49	6	9

[a] Tetraploid plants mixed with diploid individuals in same population.

the shorter style is used as the pistillate parent. Within *O. caespitosa*, the F_1 hybrids have normal meiosis and generally form seven bivalents at metaphase I (Table 8). The few exceptions to this were all cases where one of the parents was heterozygous for one translocation, suggesting that the two strains may share one common chromosome arrangement. Pollen stainability of the hybrids was typically over 80%. The only combination not obtained was between *O. caespitosa* subspp. *navajoensis* and *crinita*. This cross could be attempted only a few times because the parents were not growing well in cultivation.

Within *Oenothera caespitosa*, the phenotypes of F_1 hybrids were not intermediate for all characters. Especially notable were pubescence characters. Both the specialized villous type of pubescence characteristic of *O. caespitosa* subsp. *navajoensis* and the appressed type characteristic of subsp. *caespitosa* dominate in hybrids involving plants with a hirsute pubescence.

Within the *Oenothera caespitosa* group, nearly all interspecific combinations attempted produced F_1 hybrids with varying degrees of difficulty (Table 9). Hybrids involving *Oenothera caespitosa*, *O. harringtonii*, and *O. psammophila* have normal meiosis, form seven bivalents at metaphase I, and generally have over 70% pollen stainability. There are, however, some apparent incompatibilities in some combinations of these species, the basis of which has not been determined. Some hybrids between *O. harringtonii* and most subspecies of *O. caespitosa* were weak with slow-greening plastids. F_1 hybrids between *L. harringtonii* and *L. caespitosa* subsp. *crinita* had only 11% pollen stainability. Hybrids between *L. harringtonii* and *L. psammophila*, which were difficult to obtain, were also slow to green; none of them survived long after the initiation of flowering. The combination of *O. caespitosa* with *O. psammophila* produced similarly weak plants, but they were fully green. One hybrid between *O. harringtonii* and *O. psammophila* had seven bivalents with high pollen fertility, while another had a minimum of two translocations ($3_{II} + 2\odot 4$) and lowered pollen fertility. This result suggests that there is more than one chromosomal end arrangement within *O. psammophila*. In summary, however, there appears to be one single common chromosomal arrangement in all subspecies of *O. caespitosa* as well as in *O. psammophila* and *O. harringtonii*, with other arrangements local and not shown to be characteristic of any entire natural population within this group.

Hybrids between *Oenothera brandegeei* and *O. caespitosa* are vegetatively vigorous, but virtually sterile (mean of 1% fertile pollen). One of the F_1 hybrids had a meiotic configuration of $1_{II} + 3\odot 4$, indicating that its parents differed by at least three reciprocal translocations. A second hybrid produced by W. Stubbe (pers. comm.) had a meiotic configuration of $1_{II} + \odot 8 + \odot 4$, indicating that its parents differed by at least four reciprocal translocations. Whether this difference is related to chromosomal heterozygosity in the parents is not known. In any event, it is clear that the chromosomes of the derived annual *O. brandegeei* have been substantially rearranged as compared with those of *O. caespitosa*

and its very close relatives *O. psammophila* and *O. harringtonii*, suggesting that it was derived by saltational speciation similar to that so richly documented by Lewis and his students for *Clarkia* (also tribe Onagreae).

Hybrids between *O. harringtonii* and *O. brandegeei* were rather difficult to obtain and died soon after germination. All attempts to cross *O. brandegeei* with *O. cavernae* and *O. psammophila* failed. *Oenothera cavernae* has been successfully crossed with great difficulty to *O. caespitosa* on two occasions. The hybrids obtained were vigorous and fully green, but produced only small buds which soon aborted. Thus the chromosomal configuration of *O. cavernae* relative to that of the other species of the group unfortunately is unknown, but it may have been derived from *O. caespitosa* in a manner similar to that of *O. brandegeei*, probably independently, as suggested by Raven (1970).

Species of the *Oenothera caespitosa* group also were crossed to species that appear to be related on the basis of morphological criteria, especially seed characters. None of the 113 attempts produced any hybrids (Table 10). In some cases, however, seed was obtained but the embryos had aborted at some point during development. A similar result was found in crosses involving *O. caespitosa* with *O. macrosceles*, *O. muelleri*, or *O. primiveris*, and also crosses between *O. harringtonii* and *O. primiveris*. Stubbe (pers. comm.) obtained nearly albino seedlings following hybridization between *O. acaulis* (sect. *Lavauxia*) and *O. caespitosa*, but these soon died. These results show that the *O. caespitosa* complex is well differentiated from any other group of species in the genus.

A summary of results of the crossing program is presented in Figure 95. The internal barriers, coupled with the strong ecological differentiation discussed earlier, seem sufficient to account for the lack of naturally occurring hybrids in areas where *O. caespitosa* grows within a few meters of *O. cavernae*, *O. psammophila*, or *O. harringtonii* in adjacent habitats.

The subspecies of *Oenothera caespitosa*, together with the closely related *O. harringtonii* and *O. psammophila*, constitute a hologamodeme in the sense of Gilmour and Heslop-Harrison (1954). This high interfertility provides a tremendous potential for recombination (Epling, 1947; Anderson & Stebbins, 1954; Raven, 1980) within the limits of geographical constraints. A group of differentiated populations that can occasionally recombine their genes gives a far greater number of potential genotypes than would otherwise be possible. Some of these may be able to colonize new habitats beyond the geographical or ecological ranges of either parent. Hybridization seems to occur wherever the ranges of any of the subspecies of *O. caespitosa* overlap. This ability to hybridize may have been very important in the evolution of new forms in the *O. caespitosa* complex as the semiarid habitats of western North America changed drastically over the past several million years.

In summary, the following conclusions can be made from the experimental program:

(1) All plants examined in the *Oenothera caespitosa* complex were diploid, $n = 7$, or tetraploid, $n = 14$. Only nine collections or 14% of the total sample were tetraploid. Tetraploid plants were found in *O. caespitosa* subspp. *macroglottis*, *navajoensis*, and *crinita*. All were morphologically indistinguishable from diploid plants of the same subspecies.

(2) Translocation heterozygosity is uncommon in the group; only six plants, five of *O. caespitosa* subsp. *marginata* and one of subsp. *caespitosa* were heterozygous for one reciprocal translocation.

(3) Fully fertile F_1 hybrids can be easily obtained between the subspecies of *Oenothera caespitosa* in most combinations. This ability to hybridize may have been very important in the evolution of new forms in the *O. caespitosa* group.

(4) F_1 hybrids with generally over 70% pollen stainability can be obtained between *O. caespitosa*, *O. harringtonii*, and *O. psammophila*. Many of the hybrids, however, were slow growing or weak with slow-greening plastids.

(5) There appears to be a single common chromosome arrangement in all subspecies of *O. caespitosa* as well as in *O. psammophila* and *O. harringtonii* with other arrangements local in some populations.

(6) F_1 hybrids can be obtained between *O. caespitosa* and the two annuals, *O. cavernae* and *O. brandegeei*. The former never flowered and the latter were highly sterile. The chromosomes of *O. brandegeei* differ from *O. caespitosa* by at least 3–4 translocations, suggesting that it was derived by saltational speciation including extensive chromosomal repatterning, as suggested by Raven (1970). *Oenothera cavernae* was probably independently derived in a similar manner, but the chromosomal configuration unfortunately is not known.

TABLE 8. Summary of experimental intraspecific hybridizations within the *Oenothera caespitosa* group. NA = data not available.

Cross	Number of Attempts	% Crosses Producing Seed	% Seed Viable	Meiotic Configurations	Stainable Pollen: Number of Plants Examined	Stainable Pollen: % Range	Stainable Pollen: % Mean	Notes
O. brandegeei								
× *O. brandegeei* (self)	55	90	NA					
O. caespitosa								
Subsp. *caespitosa*								
× *caespitosa* (self)	27	0	NA					
× *caespitosa* (interpopulation)	28	82	NA	7_{II}, 5_{II} + ⊙4	4	88–95	88	Subsp. *caespitosa* parent chromosomally heterozygous.
× *crinita*	4	100	50	Not determined				Leaf shape more like subsp. *crinita*; pubescence variable.
× *macroglottis*	30	80	16	7_{II}, 5_{II} + ⊙4	5	75–96	86	Pubescence more like subsp. *caespitosa*; subsp. *caespitosa* parent chromosomally heterozygous.
× *marginata*	72	77	18	7_{II}, 5_{II} + ⊙4	11	50–95	81	Pubescence mostly like subsp. *caespitosa*; subsp. *caespitosa* parent chromosomally heterozygous.
× *navajoensis*	20	75	17	7_{II}	3	57–97	80	Pubescence like subsp. *caespitosa*.
Subsp. *crinita*								
× *crinita* (self)	20	0	NA					
× *marginata*	12	75	33	7_{II}	4	76–99	85	Robust.
× *macroglottis*	5	80	0	Not determined	1	66–88	74	Leaf shape more like subsp. *macroglottis*; pubescence more like subsp. *crinita*.
× *navajoensis*	2	0	NA					
Subsp. *marginata*								
× *marginata* (self)	105	0	NA					

TABLE 8. (Continued).

Cross	Number of Attempts	% Crosses Producing Seed	% Seed Viable	Meiotic Configurations	Stainable Pollen: Number of Plants Examined	Stainable Pollen: % Range	Stainable Pollen: % Mean	Notes
× *marginata* (interpopulation)	28	82	16	7_{II}	3	96–100	97	
× *macroglottis*	21	81	25	7_{II}, 5_{II} + ⊙4	5	75–87	79	Capsule features more like subsp. *marginata*; subsp. *marginata* parent not examined cytologically.
× *navajoensis*	21	75	38	7_{II}	51	52–93	75	Leaf and pubescence more like subsp. *navajoensis*.
Subsp. *macroglottis*								
× *macroglottis* (self)	116	80	NA					
× *macroglottis* (interpopulation)	22	82	14	7_{II}				
× *navajoensis*	11	64	33	Not determined				
Subsp. *navajoensis*								
× *navajoensis* (self)	27	0	NA					
O. cavernae								
× *O. cavernae* (self)	35	100	NA					
O. harringtonii								
× *O. harringtonii* (self)	45	0	NA					
× *O. harringtonii* (interpopulation)	9	78	0	7_{II}	3	90–97	93	
O. psammophila								
× *O. psammophila* (self)	25	0	NA					

[a] Unless otherwise noted, hybrid phenotypes were morphologically intermediate.

TABLE 9. Summary of experimental intraspecific hybridizations among species of the *Oenothera caespitosa* group. NA = data not available.

Species	Number of Attempts	% Crosses Producing Seed	% Seed Viable	Meiotic Configurations	Stainable pollen: Number of Plants Examined	Stainable pollen: % Range	Stainable pollen: % Mean	Notes
O. brandegeei				1_{II} + 304				
× *O. caespitosa*				1_{II} + 304[a]				
Subsp. *marginata*	48	44	16	1_{II} + 08 + 04[a]	7	0–2	1	Generally much like *O. brandegeei* in appearance.
× *O. cavernae*	2	98	NA					
× *O. harringtonii*	10	50	45	Not determined				Weak; died after two weeks.
× *O. psammophila*	5	0	NA					
O. cavernae								
× *O. caespitosa*								
Subsp. *caespitosa*	2	0	NA					
Subsp. *crinita*	3	0	NA					
Subsp. *marginata*	15	27	13	Not determined				Vigorous, full green; hybrids have not flowered; habit of *cavernae*.
O. harringtonii								
× *O. caespitosa*								
Subsp. *crinita*	95	82	18	Not determined	1	11	11	In all hybrids with *O. caespitosa*, pubescence generally more similar to *O. harringtonii*; plants often weak, pale green plastids slow to green. Subsp. *marginata* was chromosomally heterozygous.
Subsp. *marginata*				7_{II}, 5_{II} + 04	16	36–100	80	
Subsp. *macroglottis*				7_{II}	7	63–95	80	
Subsp. *caespitosa*					3	52–93	72	
× *O. psammophila*	17	41	0	7_{II}	–	–	–	Plants without glandular exudate, often with some hybrids yellowish green; all weak and do not survive long after flowering.
				3_{II} + 204	3	40–50	45	
O. psammophila								
× *O. caespitosa*	58	31	2	7_{II}	6	60–93	81	Without glandular exudate of *O. psammophila* and with some hairs; plants weak.

[a] Results from crosses made by W. Stubbe in Düsseldorf in 1975.

TABLE 10. Experimental interspecific hybridizations between *Oenothera caespitosa* group and related species. NA = data not available.

Species	Number of Attempts	% Crosses Producing Seed	% Seed Inviable
O. macrosceles × *O. caespitosa*	19	11	11
× *O. harringtonii*	7	0	
× *O. psammophila*	5	0	
O. muelleri × *O. caespitosa*	18	31	31
× *O. harringtonii*	5	0	
× *O. psammophila*	4	0	
O. primiveris × *O. caespitosa*	40	20	20
× *O. harringtonii*	10	30	30
O. xylocarpa × *O. caespitosa*	5	0	
O. acaulis × *O. caespitosa*[a]	NA	NA	NA

[a] Cross made by W. Stubbe in Düsseldorf in 1975.

(7) No hybrids were obtained between members of the *O. caespitosa* group and other species of the genus.

NATURAL HYBRIDIZATION

Most of the taxa in the *Oenothera caespitosa* complex have ranges that overlap with at least one other member of the group; however, intermediates have been detected only among the subspecies of *O. caespitosa.* The absence of natural hybrids between *O. caespitosa* and the specialized *O. psammophila, O. harringtonii,* and *O. cavernae* is presumed to be primarily due to the extreme ecological differences between them, and secondarily because of the weakness or high sterility of hybrids as obtained in the experimental crossing program. In contrast, intermediates are known from nearly all areas of geographical overlap among the five subspecies of *O. caespitosa.* The widespread *O. caespitosa* subsp. *marginata* intergrades with each of the other four subspecies in areas where their ranges overlap. Populations of apparent hybrid origin are also known between *O. caespitosa* subspp. *crinita* and *caespitosa* in northern Nevada, although the parents do not, as far as known, presently occur sympatrically with the intermediates. These intermediates range from sporadic hybrids, as is the case between subsp. *marginata* and subspp. *caespitosa* or *navajoensis,* which occur predominantly in disturbed sites in the presence of populations of both parents, to large hybrid zones, such as between subsp. *marginata* and subspp. *crinita* or *macroglottis,* where intergradation is virtually complete and neither parent is immediately present in its typical form.

Because hybrids between the subspecies are fully fertile, and share similar chromosomal end arrangements, the detection of hybrids depends entirely upon morphological evidence supplemented by ecological data and their distribution and abundance within populations. Morphological study of herbarium material was the primary basis for estimating the full extent of hybridization between any of the taxa. A combination of many characters was used to detect probable hybrids, in particular, maximum leaf length, floral tube length, pubescence type (e.g., villous versus hirsute), and features of the capsule and seed. When considered collectively, these characters are usually sufficient to detect putative hybrids. Careful study of the distribution and abundance of intermediates in populations was also very useful. Wagner made field studies on the pattern of hybridization of *Oenothera caespitosa* subsp. *marginata* with subspp. *caespitosa, macroglottis,* and *crinita,* and of subsp. *crinita* with subsp. *caespitosa.* A limited number of plants have also been grown from seed collected from parents and intermediates in the field, in order to sample the arrays of phenotypes produced. The specific details for hybridization between each combination of subspecies are presented in the appendix. Here only the general patterns and a few specific examples will be discussed.

The degree to which hybridization has affected sympatric populations or those that were in the past appears to be primarily dependent upon the degree of edaphic isolation or other habitat dif-

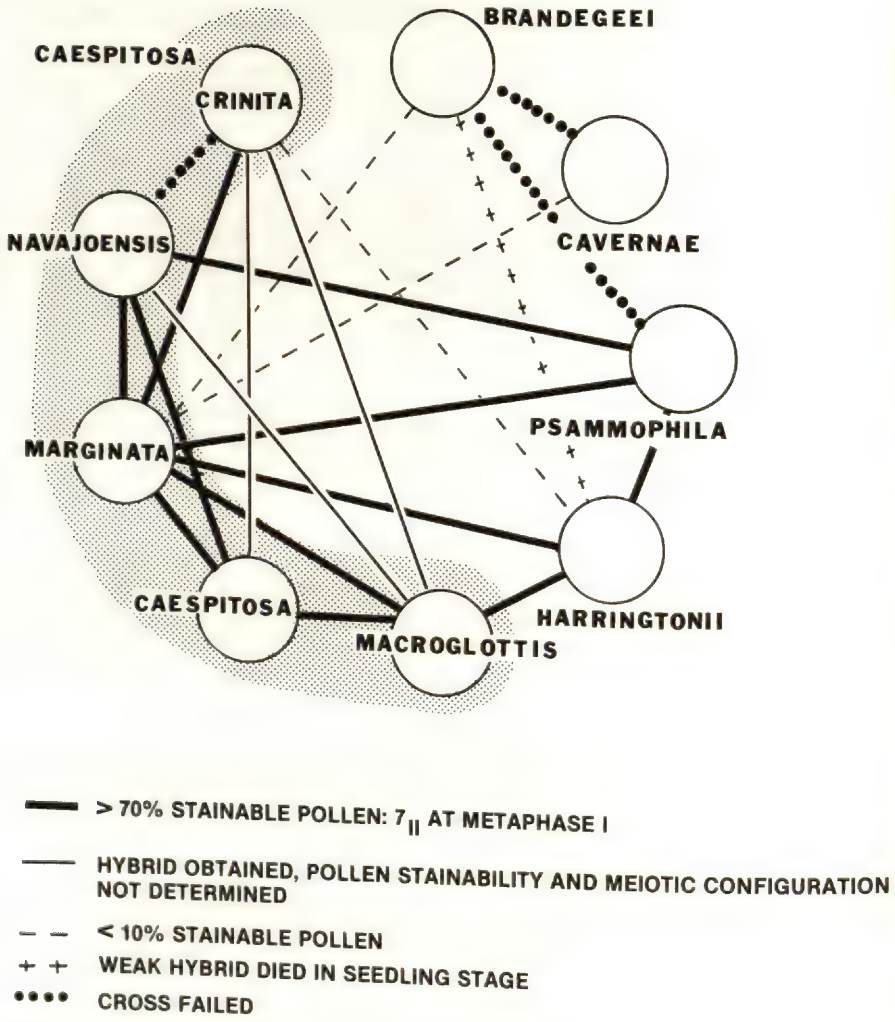


FIGURE 95. Crossing diagram.

ferences between the parent subspecies and only secondarily on spatial or temporal factors. Further, the establishment of hybrids appears to require local disturbance whereas the spread of hybrid derivatives usually seems to require climatic or geologic alterations. The various intergradation patterns between the subspecies of *O. caespitosa* appear to represent different stages in this process.

Intermediates between *Oenothera caespitosa* subsp. *marginata* and subspp. *caespitosa* and *navajoensis* appear to primarily represent products of recent localized hybridization events. The areas where the range of subsp. *marginata* overlaps with those of the other two subspecies are geologically complex. In these areas subsp. *marginata*, which occurs predominantly on relatively coarse soils, is always edaphically isolated from subspp. *caespitosa* and *navajoensis*, which both occur on much finer substrates such as fine shales or clays. This pattern can be illustrated by examples from detailed field studies of areas of sympatry between subspp. *marginata* and *caespitosa* in Utah and Wyoming.

In addition to the edaphic isolation mentioned above for *Oenothera caespitosa* subspp. *marginata* and *caespitosa*, they are also somewhat isolated in their flowering periods, for that of subsp.

marginata starts several weeks prior to that of subsp. *caespitosa* at any particular site. The flowering periods do, however, overlap broadly. In spite of these factors, which limit the extent of hybridization, the two subspecies produce hybrids in areas of sympatry. The intermediates are mainly confined to disturbed sites, such as roadcuts or other open disturbed sites. In all areas studied both parents could be found in the immediate vicinity of the hybrids. The hybrid plants are always rare while the parents usually are much more common. In spite of the widespread occurrence of fertile hybrids between subspp. *marginata* and *caespitosa* there appears to be, in general, a limited amount of backcrossing or interhybrid crossing, and it does not appear to have led to the development of large hybrid swarms. These generalizations can be illustrated by two specific examples.

At a site on the lower slope in the vicinity of Two Jump Canyon, Wellsville Mountains, Box Elder County, Utah, *Oenothera caespitosa* subspp. *marginata* [*Wagner 4065* (MO)] and *caespitosa* [*Wagner 4066* (MO)] grow within 100 m of each other. Subspecies *caespitosa* was restricted to limestone and shale cliffs and the talus below, whereas subsp. *marginata* was common on the upper bajadas, where the soil is a mixture of weathered granite and some shales. One plant [*Wagner 4064* (MO)], growing in a horse corral within a population of subsp. *marginata,* had an odd combination of characters of both subspecies. It had the leaf shape and lobing pattern, capsule shape, and internal ribbing of the seed-collar of subsp. *caespitosa,* and the hirsute pubescence, glandular hairs, pedicellate capsules, and reticulate seed coats of subsp. *marginata.* This morphology is not the same as that of artificially produced F_1 hybrids and the plant seems to represent a backcross to subsp. *marginata.* Progeny grown from seed collected from this individual were viable and they were much more similar to subsp. *marginata* than to subsp. *caespitosa.* Out of ten individuals grown, several had unusual phenotypes intermediate for leaf shape and pubescence. In other characteristics, however, such as capsule shape, long pedicels, and most seed coat characters, they consistently resembled subsp. *marginata.* The seed-collars, however, consistently had small internal ribs, a character of subsp. *caespitosa.* Several other plants growing along a small wash within the population of subsp. *marginata* had phenotypes similar to the greenhouse progeny grown from the horse-corral plant. Besides the horse-corral plant and those along the wash, all other individuals in the area easily could be placed into one or the other subspecies. Upon close examination, however, some characteristics of the other subspecies were detected even in some of these plants. Seeds of four plants of subsp. *marginata* were typical except that all had the internal ribbing in the seed-collar characteristic of subsp. *caespitosa.* In contrast, some plants that closely resembled subsp. *caespitosa* in most respects had leaves that sometimes approached those of subsp. *marginata* in their lobing pattern. In addition, the length of the strigillose pubescence on the leaves was often more variable on certain individuals than is normally expected. The hairs were sometimes up to 1 mm long rather than the typical range of 0.2–0.6 mm. Neither subspecies was in flower, so floral characters could not be studied directly. Judged from the herbarium material from that general part of Utah, the flower fading color and floral tube lengths also seem to be affected to some degree by hybridization.

A similar pattern was observed on two extensive roadcuts in Lincoln County, Wyoming (*Wagner 4054, 4057*). The basic difference between this site and the Utah site was the much greater degree of disturbance. *Oenothera caespitosa* subsp. *marginata* was fairly common on sandy soils in the adjacent sagebrush scrub, but *O. caespitosa* subsp. *caespitosa* was confined to a small shale outcrop that was contiguous with the roadcut. Although most individuals showed a strong resemblance to one or the other parental phenotype, most individuals growing on the roadcut showed some evidence of hybridization. Only relatively few individuals (e.g., *Wagner 4054C*), however, closely matched artificially produced F_1 hybrids. By far, most individuals had one or two features of the other subspecies. For example, the following recombinant phenotypes were observed:

(a) Plants with the leaf shape and lobing, pubescence, capsule shape and tubercles of subsp. *marginata,* but with the ribbed inner wall of the seed-collar of subsp. *caespitosa* (*Wagner 4054C*; also a common phenotype at Wellsville, Utah, site).
(b) Plants similar to those in (a) but with the smooth inner seed-collar walls of subsp. *marginata,* and with the papillose seed surface of subsp. *caespitosa* (*Wagner 4054D-1*).
(c) Plants similar to those in (a) but with cap-

sules somewhat falcate as in subsp. *caespitosa* (*Wagner 4054D-1*).

(d) Caespitose-like plants with intermediate capsules but typical seed morphology (*Wagner 4054A*).

A very similar pattern of local hybridization was found between *Oenothera caespitosa* subspp. *marginata* and *navajoensis*. These two subspecies are apparently more strongly isolated edaphically and temporally in that subsp. *navajoensis* flowers somewhat earlier than subsp. *marginata*. Their flowering periods, however, do overlap. Intergradation between these subspecies was not studied in detail in the field and the details given in the appendix were based largely on the study of herbarium material.

The second pattern of intergradation between the subspecies of *Oenothera caespitosa* is one of almost complete intergradation over wide areas and apparently results from weak ecological isolation between the subspecies involved. This pattern is represented by interactions between subsp. *marginata* with subspp. *macroglottis* and *crinita*. In areas of geographical overlap, subsp. *marginata* is isolated from these two subspecies primarily altitudinally. The products of this are variable populations that gradually replace each other morphologically in intermediate altitudinal zones. In some instances, plants from certain populations may be difficult to assign to one or the other subspecies. Extremely variable populations of *O. caespitosa* subsp. *crinita*, in which some individuals morphologically approach subsp. *marginata*, occur in low elevation Mojave Desert scrub habitats in Inyo County, California. Populations morphologically typical of subsp. *marginata* can be found at higher elevations in a majority of the regional mountains on limestone substrates. The great increase in aridity in this area during the last 10,000 years probably has been important in the spread of these variable populations of subsp. *crinita*.

In the Charleston Mountains in southern Nevada, where both subspecies occur, they apparently have hybridized with a different result. Populations of *Oenothera caespitosa* subsp. *marginata* are much smaller and more variable in leaf and floral-tube lengths than are other populations in the region. This variation was perhaps introduced by past hybridization with *O. caespitosa* subsp. *crinita*. Further details of this situation are given in the appendix.

In Colorado and northern New Mexico, where the vegetation has been less severely altered during the last 10,000 years, there is a rather smooth morphological transition between *Oenothera caespitosa* subsp. *marginata*, found in the pinyon-juniper woodlands and Great Basin scrub, and *O. caespitosa* subsp. *macroglottis*, found in coniferous forests. None of the transitional populations display the great amounts of variability exhibited by the low elevation California populations of *O. caespitosa* subsp. *crinita*.

The final pattern of intergradation found between the subspecies of *Oenothera caespitosa* consists of a series of relatively uniform intermediate populations with discrete geographical and/or ecological ranges; all of them appear to have had a hybrid origin. Although it is virtually impossible to prove this, several lines of evidence support the hypothesis of a hybrid origin rather than one of primary divergence. Morphologically intermediate populations are either primitively intermediate, having obtained those particular features prior to the origin and spread of the divergent forms, or they are secondarily intermediate, having obtained them following hybridization between morphological extremes. Three lines of evidence support the hypothesis of secondary contact: (1) Intermediates between *O. caespitosa* subsp. *marginata* and each of the other four subspecies occur in a number of different, often widely separated areas. If a pattern such as this could be explained by one of divergence then it would be more likely to find the intermediates in only one geographical area. (2) Many of the intermediate populations possess derived characters of both taxa, as discussed in the next section. (3) Intermediates from different geographical areas often have different combinations of characters of the extreme forms. The first point alternatively could be interpreted as relictual populations of a more widespread entity, but the latter two points strongly support the argument.

Many of the geographical areas where these intermediate forms occur no longer have habitats that would support one or both of the putative parents, but based largely on packrat midden analysis, they did have such habitats as recently as 8,000 to 12,000 years ago. These intermediates seem to have originated at many different times during the evolutionary history of the group.

Several examples, each discussed at length in the appendix, demonstrate the overall patterns. Here two of the clearest and most striking examples will be given. In Elko and Humboldt

Counties in northern Nevada, there are populations intermediate between *O. caespitosa* subspp. *caespitosa* and *crinita*. The plants of these populations, which occur from 1,200 to 1,700 m elevation in Great Basin Desert scrub, are *caespitosa*-like but also have some *crinita*-like features, in that they have at least some spreading hairs over 0.6 mm long as well as glandular hairs on their floral tubes. Populations quite typical of subsp. *caespitosa* occur in the same region, but only at higher elevations, mostly above 2,400 m, in the isolated mountains on exposed limestone and shale ridges. On the other hand *O. caespitosa* subsp. *crinita*, near its northern limit in northern Nevada, occurs in scattered populations in Great Basin scrub and pinyon-juniper woodlands. Thus the intermediates occur in more arid habitats than does either putative parent; the arid habitats in which they occur have become extensive only during the past 10,000 years. The variable, and intermediate, plants are presumably the result of widespread hybridization in the past. In the past when the region was moister, populations of *O. caespitosa* subsp. *crinita* may have been in close contact with those of subsp. *caespitosa*. Low-elevation populations of both subspecies were largely replaced in spreading drier sites by intermediates. *Oenothera caespitosa* subsp. *caespitosa* has persisted only in cooler and more mesic sites in many of the isolated mountains of the area.

Another series of plants that may have had a hybrid origin is known from Laramie County, Wyoming, and adjacent Logan and Weld Counties, Colorado. These plants also resemble *Oenothera caespitosa* subsp. *caespitosa*, but are atypical in having long, spreading, somewhat crinkly hairs and small leaves, flowers, and fruit. The hairs are very similar to those of *O. caespitosa* subsp. *macroglottis* which is at its northeastern limit in this area. *Oenothera caespitosa* subsp. *caespitosa* generally grows on heavy clay soils, whereas subsp. *macroglottis* occurs in much coarser soils with higher sand and gravel content. The soils where two populations of the long-haired form was growing were intermediate or varied toward substrates similar to those of *O. caespitosa* subsp. *macroglottis*. Neither of the putative parents could be located near any of the populations studied, but this long-haired form is positioned geographically between the ranges of the two subspecies as well as growing in intermediate substrates.

Other instances in which two subspecies have formed intermediate populations are known between *Oenothera caespitosa* subspp. *marginata* and *navajoensis* in volcanic cinders in northern Arizona; subspp. *marginata* and *macroglottis* on the Mogollon Rim in Arizona; and two areas in northern Nevada that involve *O. caespitosa* subspp. *crinita* and *marginata*, but in which intermediate populations, putatively of hybrid origin, appear to have become characteristic of extensive areas.

We have demonstrated in this section that whenever the subspecies of *Oenothera caespitosa* come into close contact they hybridize. These events range from sporadic hybrids which occur predominantly in recently disturbed habitats in the presence of the parents to large hybrid zones where intergradation is complete and neither parent is present in the typical extreme form or intermediate populations that inhabit sites with one or both parents absent from the region. The intermediates in the latter case occur in habitats, such as low elevation deserts, that did not exist as such until the last 8,000 to 10,000 years. These new forms arising through hybridization appear to have made possible the continued survival of *O. caespitosa* in these rapidly changing arid habitats. This phenomenon has also served to weaken the distinctness between the subspecies.

Evidence presented in the next section suggests, that in at least one case, hybridization was followed by the evolution of novel phenotypes in stabilized hybrid derivatives. *Oenothera psammophila* may have originated via hybridization between *O. caespitosa* subspp. *marginata* and *caespitosa*. With the exception of unique characters all of its features are shared with one or the other of these two subspecies.

Cladistic Analysis

In this section the relationships among the members of the *Oenothera caespitosa* species group will be examined. Four other species, *O. macrosceles*, *O. muelleri*, *O. primiveris*, and *O. xylocarpa*, are also included in the analysis because they are hypothesized as being the extant species most closely related to the *O. caespitosa* group. These four species, based on the absence of certain derived characters, are clearly not members of the *O. caespitosa* group, but their inclusion provides a conceptual framework within which to view the relationship of the *O. caespitosa* group to the remainder of the genus.

There are a number of reasons for performing

a cladistic analysis. First, and perhaps foremost, this methodology provides a means to clearly state the hypotheses, based on shared derived characters (synapomorphies) and their underlying assumptions, which are the basis for our understanding of evolutionary relationships. Moreover, since a hypothesis is clearly stated for each character it is relatively easy to detect contrasting hypotheses, which can be tested by further in-depth rigorous studies. Second, much more information is maintained in retrievable form than by other less formal approaches. Finally, a more precise and objective methodology allows one to escape from a priori judgements made about the groups being studied, and forces a critical examination of each character independently, as well as revealing new ones.

The data were analyzed by a computer parsimony program, "Wagner 78," written by J. S. Farris and run at the University of Kansas with the aid of E. O. Wiley. This Wagner tree program is the most recent version of the basic algorithm outlined by Kluge and Farris (1969), and produces a rooted tree. The value of the program over strictly manual solutions is as an aid in detecting homoplasy (similarity arising from convergence), especially when dealing with large data sets (Wiley, 1980). The final results presented here are less parsimonious than the computer-generated tree. Some alterations in the computer-generated tree were made to reduce the number of hypothesized character reversals where these seemed unlikely. In such cases a hypothesis that suggests that certain characteristics, presumed to be complex, were lost on two or more independent occasions was more probable than a hypothesis of reversal.

What role should this type of analysis play in the overall classification of the group? We do not agree with the idea expressed by most cladists that phylogenetic relationships be reflected *exactly* in the classification of a group. The basic problem with this idea is that it is open-ended. Since evolution operates at the population level, unique traits will arise continually in populations and often spread to series of populations (Raven, 1980). If a group is studied in enough detail, a tree for nearly all populations could be constructed. Where does one draw the line of assigning terminal groups to different formally recognized taxonomic units? In the *Oenothera caespitosa* group this approach would lead to a number of highly technical species that even a specialist would have difficulty identifying consistently. Thus the classification system would have failed in its goal as an information-retrieval system. We agree with the view expressed by Raven (1977) and others that construction of general-purpose classifications and the study of particular genetic, evolutionary, or ecological features of populations should be separate endeavors.

A second point concerns the reasons for recognizing the major morphological/geographical units in *Oenothera caespitosa* as subspecies rather than giving each of them the rank of species. The overwhelming factors in assigning subspecific or specific rank in this group was the degree of discontinuity between the population series, regardless of whether a zone of intergradation was hypothesized as primary or secondary, as well as the degree of differentiation between entities. This approach has resulted in the recognition of a species, *Oenothera caespitosa,* which is not monophyletic according to the definitions of some cladists, in which a monophyletic group is composed of an ancestral species and *all* descendants of that species (Hennig, 1966; Farris, 1974). *Oenothera caespitosa* is a paraphyletic assemblage because the strongly differentiated derived taxa *O. cavernae, O. brandegeei, O. psammophila,* and *O. harringtonii* have been excluded. We do not in general advocate the recognition of paraphyletic groups, but, at least in plants, there are certain problems where there is no classification that is completely satisfactory. Often a general-purpose classification based on morphological gaps in the variation pattern will delimit species that are monophyletic in the strict Hennigian sense. In a group where secondary contact is followed by the spread of hybrid derivatives that lack unique features, however, this can not be achieved.

The criterion for the determination of generalized (plesiomorphic) and specialized (apomorphic) states for each character is the outgroup comparison (Hennig, 1966; Wiley, 1980; Watrous & Wheeler, 1981). The primary outgroup consulted was *Oenothera* sect. *Oenothera* subsect. *Emersonia,* primarily *O. macrosceles,* but sometimes the three other species of subsect. *Emersonia* were considered. This group is hypothesized as the sister-group (sensu Hennig, 1966) to the group that consists of the *O. caespitosa* complex, *O. muelleri, O. primiveris,* and *O. xylocarpa* because of their common possession of a distal and/or raphial cavity (seed-collar) in the seed. An additional point of evidence is

that hybrids that die as seedlings have been obtained between *O. macrosceles* and *O. muelleri* (Raven, 1970).

Other sections of *Oenothera* or other genera of the tribe Onagreae were also consulted as outgroups for each character, and in two cases these comparisons suggested that the character state in the *O. caespitosa* group rather than the one in *O. macrosceles* was plesiomorphic. The most difficult problem in determining polarity is the situation in which a homologous character state cannot be determined in the outgroup; the character is confined to the group under consideration. In these situations, a functional outgroup comparison is made by determining which undirected character state is associated with one or more of the three species (i.e., *O. muelleri, O. primiveris,* and *O. xylocarpa*) that are outside the *O. caespitosa* complex but were included in the analysis. The state found in both the functional outgroup and a member of the *O. caespitosa* group is considered to be the plesiomorphic state (Watrous & Wheeler, 1981).

Thirty-six characters were utilized in the computer analysis on which the statements of relationship presented here are based. Many apomorphic characters, especially of taxa outside the *O. caespitosa* group, are excluded for the sake of clarity and because they do not contribute to any further resolution of the relationships among taxa. In the following list the character is given in italics followed by the zero-state (0) for plesiomorphic states and (1) or higher for the apomorphic state(s). A brief statement is often included explaining the basis of the polarity decision. If the hypothesis of polarity is a straightforward one based solely on outgroup comparison to *O. macrosceles* no comment is given. The character state in each taxon for each of the 36 characters is given in the data matrix (Table 11).

1. *Taproot producing lateral roots from which adventitious shoots arise.* 0 = Present. 1 = Absent. Although *O. macrosceles* does not have the zero state, *O. maysillesii* Munz in sect. *Oenothera* subsect. *Emersonia* does. In addition, species of sect. *Megapterium* and sect. *Lavauxia* also reproduce by this means.
2. *Stems.* 0 = Many, prostrate, creeping from a central rosette. 1 = Ascending, erect or absent, rosette present.
3. *Leaves, buds, and/or capsules with reddish purple splotches.* 0 = Present. 1 = Absent.
4. *Pubescence of minute glandular hairs.* 0 = Present. 1 = Absent. Also present in most other genera of the family.
5. *Pubescence.* 0 = Hirsute or absent. 1 = Villous.
6. *Pubescence.* 0 = Hirsute or absent. 1 = Strigillose. Outgroup comparison. Crosses between hirsute and strigillose gave one intermediate phenotype, a result that suggests that strigillose is not homologous with appressed pubescence in character 9.
7. *Pubescence.* 0 = Hirsute or absent. 1 = Hirtellous.
8. *Pubescence.* 0 = Hirsute or absent. 1 = Crinkly hirsute.
9. *Pubescence of short slender appressed hairs or in* O. xylocarpa *spreading.* 0 = Present. 1 = Absent.
10. *Flowering from rosette.* 0 = Absent. 1 = Present.
11. *Bud cross-section.* 0 = Obscurely quadrangular. 1 = Conspicuously quadrangular.
12. *Buds.* 0 = With free sepal-tips. 1 = Without free sepal-tips.
13. *Petal color.* 0 = Yellow. 1 = White.
14. *Petals faded color.* 0 = Orange red or salmon red. 1 = Deep purple to rose. 2 = Pink to lavender or pale rose. Outgroup comparison. For the polarity of 1 and 2 a functional outgroup, *O. primiveris* was used (i.e., the petals of both *O. primiveris* and some members of the *O. caespitosa* group fade deep purple to rose).
15. *Capsule pedicel.* 0 = Sessile. 1 = Present, but may be exceedingly short.
16. *Capsule base in pedicellate taxa.* 0 = Cuneate. 1 = Truncate. Functional outgroup comparison using the only pedicellate species (of those included in this study outside *O. caespitosa* group, *O. xylocarpa* (i.e., the capsules of both *O. xylocarpa* and those of most members of the *O. caespitosa* group have cuneate bases).
17. *Capsule diameter basally.* 0 = 2–3 mm. 1 = 4–8 mm.
18. *Capsule cross-section.* 0 = Conspicuously quadrangular, angles acute. 1 = Obscurely quadrangular, angles obtuse.
19. *Capsule apex.* 0 = Not beaked. 1 = Beaked.
20. *Capsule symmetry.* 0 = Slightly asymmetrical. 1 = Strongly asymmetrical. 2 = Nearly symmetrical.
21. *Capsule curvature.* 0 = Arched. 1 = Falcate or sigmoid. 2 = Straight or slightly curved. Outgroup comparison. For polarity of 1 and

TABLE 11. Data matrix for characters of *Oenothera* species used in cladistic analysis.

Taxon	Characters																																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
O. macrosceles	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
O. muelleri	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
O. primiveris	1	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
O. xylocarpa	1	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	1	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0
O. caespitosa subsp. *crinita* common form	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	0/1	0	0	1	2	0	0	0/1	0	1	1
O. caespitosa subsp. *crinita* pulvinate form	1	1	0	0	0	0	0	0	1	1	1	1	1	2	1	0	1	1	1	1	2	1	1	0	1	0	0/1	0	1	2	0	0	0	0	0/1	1
O. caespitosa subsp. *caespitosa*	0	1	1	1	0	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	0	0	0	1	2	0	0	0	0	0	1
O. caespitosa subsp. *navajoensis*	0	1	0	0	1	0	0	0	1	1	1	1	1	2	1	1	1	1	1	2	2	1	1	0	1	0/1	0	0	1	2	0	1	0	0	0	2
O. caespitosa subsp. *macroglottis*	0	1	1	0	0	0	0	1	1	1	1	1	1	2	1	0	1	1	1	2	2	1	2	0	1	0	0	0	1	2	0	1	0	0	0	2
O. caespitosa subsp. *marginata*	1	1	0/1	0	0	0	0	0	1	1	1	1	1	2	1	0	1	1	1	2	2	1	2	0	1	1	0	0	1	2	0	1	0	0	0	2
O. brandegeei	1	1	0	0	0	0	0	0	1	1	1	1	1	2	1	0	1	1	1	1	1	1	1	0	1	0	1	0	1	2	0	0	0	1	1	1
O. cavernae	1	1	0	0	0	0	0	0	1	1	1	1	1	2	1	0	1	1	1	1	1	1	1	0	1	1	0	0	1	2	0	0	1	0	1	1
O. harringtonii	1	1	1	0	0	0	1	0	1	1	1	1	1	2	1	1	1	1	1	2	2	1	1	0	1	0	0	0	1	2	0	1	0	0	0	2
O. psammophila	1	1	1	1	0	0	0	0	1	1	1	1	1	2	1	0	1	1	1	2	2	1	2	0	1	1	0	0	1	2	0	1	0	0	0	1

2, functional outgroups, *O. xylocarpa, O. muelleri,* and *O. primiveris* were used (all comparisons suggest that straight capsules are the apomorphic state).

22. *Margins of capsule valves thickened into ridge or tubercles.* 0 = Absent. 1 = Present.
23. *Capsule shape.* 0 = Cylindric. 1 = Ovoid. 2 = Lance-cylindric to cylindric.
24. *Seed color.* 0 = Brown. 1 = Gray and black.
25. *Seed color and patterning.* 0 = Brown, mottled with darker purple-brown spots or gray-black modification. 1 = Reddish brown to dark purplish brown (appearing nearly black).
26. *Seed surface sculpture.* 0 = Papillose. 1 = Reticulate. Functional outgroup comparison using *O. xylocarpa* and *O. primiveris.*
27. *Seed surface sculpture.* 0 = Papillose. 1 = Roughened. Same reasoning as 26. An alternative hypothesis is that roughened is derived from reticulate.
28. *Seed surface sculpture.* 0 = Papillose. 1 = Elongate flattened papillae. Same reasoning as 26.
29. *Seed surface microsculpture.* 0 = Smooth at 250×. 1 = Micropapillae present.
30. *Distal end and/or adaxial side of seed.* 0 = With a distal cavity. 1 = *O. primiveris* type seed-collar. 2 = *O. caespitosa* type seed-collar.
31. *Seed-collar.* 0 = Present. 1 = Vestigial.
32. *Seed-collar membrane.* 0 = Depressed into groove and splitting at maturity or absent. 1 = Not strongly depressed and usually intact at maturity. A functional outgroup comparison was made using *O. muelleri* and *O. primiveris,* the only other taxa with seed-collars other than the *O. caespitosa* group.
33. *Seed-collar membrane.* 0 = Present. 1 = Absent. Same functional outgroups as 32.
34. *Seed-collar.* 0 = Normal. 1 = Collar rolled out from center and collar filled with large cells with internal thickenings. Same functional outgroups as 32.
35. *Seed-collar margin.* 0 = Sinuate distally or entire. 1 = Sinuate throughout. Same functional outgroups as 32.
36. *Internal features of seed-collar.* 0 = Completely filled with large cells. 1 = With transverse ribs and partial filled with large cells. 2 = Cells of collar smaller and internal wall smooth.

The cladogram that best reflects our present hypotheses of relationship is presented in Figure 96. *Oenothera muelleri, O. primiveris, O. xylocarpa,* and the *O. caespitosa* group constitute a monophyletic group. In the cladogram the most distinctive synapomorphy is the possession of a seed-collar (Character 30). Other synapomorphies are: sepals lacking free tips in bud (Character 12), faded petals rose or purple (Character 14), asymmetrical capsules (Character 20), broad based capsules (Character 17), and micropapillose seed surface (Character 29). Each of these last five mentioned characters, however, is known elsewhere in the genus and thus must have evolved independently on several occasions. This monophyletic group was discussed in the context of sect. *Pachylophus* by Raven (1970), who also included *O. macrosceles,* which has since been placed in sect. *Oenothera* subsect. *Emersonia* (Stubbe & Raven, 1979). According to the cladogram (Fig. 96), the group is subdivided into four monophyletic groups with *O. primiveris* and *O. xylocarpa* being especially close to one another. In fact, closer study of these two species may show them to possess at least some synapomorphies. Conspicuously quadrangular buds (Character 11), white petals (Character 13), and obtusely angled capsules (Character 18) are hypothesized as evolving independently in *O. muelleri* and the *O. caespitosa* group. The alternative hypothesis, reversing the positions of *O. muelleri* and *O. primiveris* along with *O. xylocarpa,* is represented in Figure 97. This alternative hypothesis requires the acceptance of a much higher degree of homoplasy, and seems less likely than the former hypothesis where there are only three parallelisms. Each of the four monophyletic groups could be recognized at the sectional level or alternatively included in one polymorphic section as has been done in the past. The sectional classification ultimately adopted for this group should await the completion of further studies now under way (Wagner, in prep.). including additional experimental hybridizations and a detailed study of capsules and seeds in the entire genus.

The species of the *Oenothera caespitosa* complex are united by seven synapomorphies, two of which, capsule margins thickened into a ridge or a row of tubercles (Character 22) and possession of an *O. caespitosa* type seed-collar (Character 30), are unique within the genus. Character states closely similar to the other five synapomorphies have evolved independently in other sections of the genus. Nevertheless, the *O. caes-*

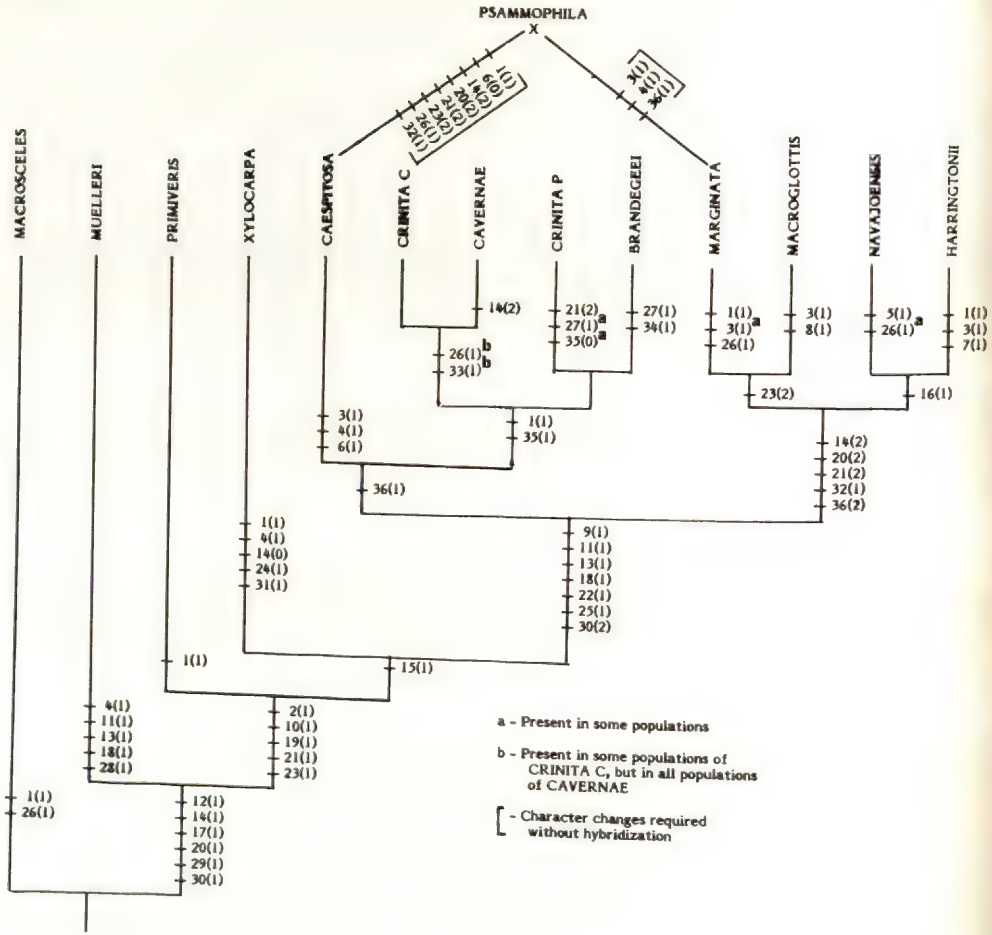


FIGURE 96. Cladogram of *Oenothera caespitosa* group and related species.

pitosa group is clearly a distinctive monophyletic group not closely related to any other taxa in the genus.

Within the *Oenothera caespitosa* group there are two groups of taxa that appear to have diverged from the common ancestor of the group early in its evolution. The branch that includes *O. caespitosa* subspp. *marginata, navajoensis, macroglottis,* and *O. harringtonii* is especially well supported by a number of synapomorphies. The smooth internal walls of the seed-collars (Character 32) seem to be true synapomorphies, while the others (Characters 14, 20, 21) are less clearly homologous or, in the case of the color of the faded petals (Character 14), independently derived at least one other time in the common ancestor of *O. brandegeei, O. cavernae,* and the pulvinate form of *O. caespitosa* subsp. *crinita.* On the other hand, the branch leading to the remaining taxa is defined by only one synapomorphy, seed-collars with internal ribbing (Character 36).

Beyond this early divergence the remainder of the tree has a marked paucity of derived characters that link any two or more taxa together. There are, however, a number of apomorphies that are unique to any particular taxon. Most of these were not included in the analysis. There are at least two possible causes that singly or together may explain this pattern. First, the hypothesized relationships may be true and there are not any characters that will further resolve

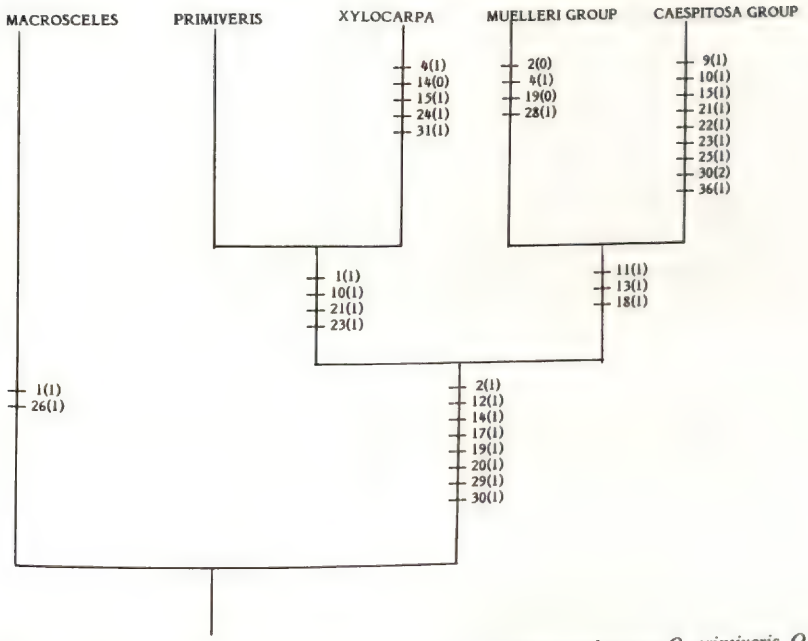


FIGURE 97. Alternative cladogram for the relationships of *Oenothera xylocarpa, O. primiveris, O. muelleri,* and the *O. caespitosa* group.

the relationships, in which case there must have been bursts of divergence in several directions from a single common ancestor at certain times in the history of the group. Another factor that undoubtedly has contributed to this situation is that there are many apparent cases of parallelism, and, based on present knowledge, the true transformation series cannot be distinguished; for this reason, most of these characters were not included in the analysis. For example, some characters such as reduction of the stems to virtual acaulescence occurred repeatedly in xeric habitats and is a character that is often quite variable even within certain populations. Another example is the absence of purple splotches on leaves and buds (Character 3). To explain the distribution of this character requires either (1) the loss of the ability to produce the pigment and its subsequent reappearance; or (2) the loss of the ability to produce the pigment on at least five separate occasions. One must hypothesize similar alternatives in the loss of the ability to produce new shoots from roots (Character 1). Thus, if character state reversals are less likely than parallel loss of those character states, then loss of character states must account for a substantial amount of the morphological divergence in this group.

The relationships of the pulvinate form of *Oenothera caespitosa* subsp. *crinita* are somewhat dubious. Its position hypothesized in Figure 96 is based primarily on the possession of internal ribbing in the seed-collars (Character 36). If this seed-collar morphology is a true synapomorphy rather than a parallelism then one must also consider an alternative hypothesis that places the pulvinate form on the other main branch (Fig. 98). Which of these other hypotheses may be the best estimate of relationship cannot be determined based on present information.

Another puzzling feature of the pulvinate form of *Oenothera caespitosa* subsp. *crinata* is that it is heterogeneous for roughened seed surface (Character 27) and seed-collar margins sinuate throughout (Character 35). High-elevation populations of the pulvinate form have one set of characters states [27(1), 35(0)], while low-elevation populations restricted to extreme white chalky calcareous substrates have the alternate set [27(0), 35(1)]. The common form of *O. caespitosa* subsp. *crinita* has similar dual character states for seed sculpturing (Character 26; reticulate or papillose) and seed-collar membrane (Character 33; present or absent). Both of these dual states may be explained easily. The genetic control of seed surface sculpturing as mentioned

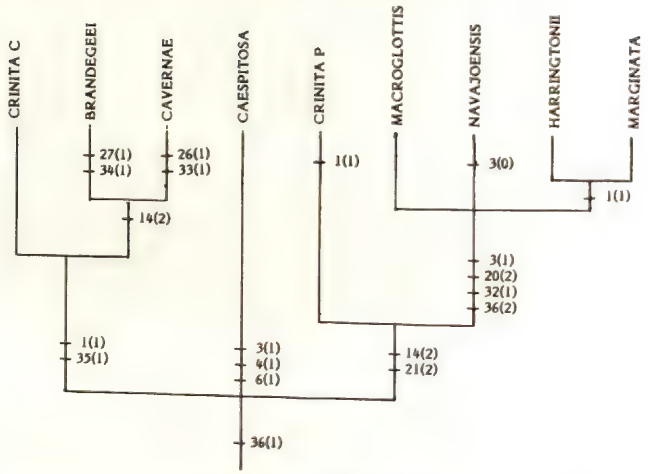


FIGURE 98. Alternative cladogram for *Oenothera caespitosa* subsp. *crinita* pulvinate form.

above and presence of seed-collar membrane may be relatively simple and a particular pattern or loss of the membrane therefore could easily evolve independently in several evolutionary lines. Alternatively, the occurrence of reticulate seed surfaces in some populations of *O. caespitosa* subsp. *crinita* and some of *O. caespitosa* subsp. *navajoensis* may be the result of past hybridization between these entities and *O. caespitosa* subsp. *marginata*.

Hybridization has played a role in the production of new adaptive recombinant genotypes in *Oenothera caespitosa*. As discussed previously, hybrid zones sometimes cover wide areas and the apparent hybrid derivatives are the only individuals persisting in certain climatically altered areas. The simplest hypothesis to explain the combination of features in *O. psammophila* is one that involves hybrid origin from *O. caespitosa* subspp. *caespitosa* and *marginata* (Fig. 96). Alternatively, divergence from one or the other subspecies would require the character-state changes enclosed in brackets. Hybrid origin requires essentially no character-state changes but rather the recombination of features that were already present in at least one of the putative parental taxa. The direct derivation of *O. psammophila* from the *O. caespitosa* subsp. *marginata* line also seems reasonable except for the presence of small internal ribs in the vestigial seed-collars (Character 36). A comparison of certain characters of these three taxa is presented in Table 12. In features such as leaf texture or length of floral tube, *O. psammophila* is very similar to *O. caespitosa* subsp. *caespitosa*, whereas in others, such as capsule shape, it more closely resembles *O. caespitosa* subsp. *marginata*. Capsule curvature and seed-surface sculpturing in *O. psammophila* are intermediate between those characteristic of the two subspecies of *O. caespitosa*. In support of the hybridization hypothesis is the observation that the wavy-ridged margin of the capsules, leathery leaf texture, and slight asymmetry of the capsules in *O. psammophila* are strikingly similar to that of some F_1 hybrids between *O. caespitosa* subspp. *caespitosa* and *marginata*. *Oenothera psammophila*, however, differs from F_1 hybrids in the dense secondary branching, decumbent stems, resinous exudate on young plant parts, vestigial seed-collar, and pustulate-reticulate seed sculpture. These features are all unique apomorphies. This evidence taken altogether supports the hypothesis of hybrid origin of *O. psammophila* followed by progressive differentiation in its unique habitat, more than any of the alternatives.

There is also a remote possibility that *Oenothera caespitosa* subsp. *macroglottis* also had a hybrid origin from *O. caespitosa* subspp. *caespitosa* and *marginata*. *Oenothera caespitosa* subsp. *macroglottis* has certain intermediate features such as wavy-ridged capsule margins, curved capsules, and color of the faded petals. However, as shown in Figure 96, *O. caespitosa* subsp. *macroglottis* could very easily have shared a common ancestor with *O. caespitosa* subsp. *marginata*,

TABLE 12. Comparison of characters of *Oenothera caespitosa* subsp. *caespitosa*, *O. caespitosa* subsp. *marginata*, and *O. psammophila*.

Character	*O. caespitosa* Subsp. *caespitosa*	*O. psammophila*	*O. caespitosa* Subsp. *marginata*
Leaf texture	Thick, somewhat leathery	Thick, somewhat leathery	Thick or thinner, not especially leathery
Leaf margin	Coarsely serrate or dentate, pinnately-lobed or subentire	Subentire to remotely dentate	Pinnately-lobed to dentate or coarsely erose
Leaf length (cm)	(2.8–)7–16(–21)	(6–)8–9(–14.2)	(2.8–)10–26(–36)
Floral tubes (cm)	(3.5–)4–6(–8.5)	4.2–6	(4.1–)8–14(–16.5)
Color of faded petals	Rose pink to rose purple	Rose pink to rose	Pink to lavender
Capsule shape	Lanceoloid to ovoid	Lance-cylindric	Cylindric to lance-cylindric
Capsule curvature	Falcate or sigmoid	Curved	Straight
Capsule margin	Tuberculate or sinuate-ridged	Wavy ridge	Tuberculate or sinuate-ridged
Seed surface sculpturing	Papillose	Pustulate-reticulate	Reticulate
Seed-collar membrane	Split at maturity	Intact at maturity	Intact at maturity

with the intermediate features being parallelisms.

Finally, some characteristics have clearly been derived on numerous occasions and are therefore considered to be unreliable for cladistic analysis. For example, self-incompatibility has been lost on numerous occasions in some taxa or populations of some taxa in nearly every group of Onagraceae that has a self-incompatibility system (Raven, 1979). Thus self-compatibility cannot be considered to be a reliable synapomorphy to link *O. brandegeei* and *O. cavernae*, and neither can the reduction in flower size characteristic of these autogamous entities. Similarly, the annual habit cannot be used. On the other hand, floral fragrances would probably be very useful, but they need to be characterized chemically. There are four basic fragrances in the group of taxa considered: (1) pungent, with a semen-like background odor (*O. macrosceles*, weak, and *O. primiveris*, strong); (2) sweet with a peppery background odor (*O. muelleri*); (3) sweet with a background odor of rubber (*O. caespitosa* group); and (4) intensely sweet (*O. xylocarpa* and some *O. primiveris*). Based on proposed relationships in the cladogram sweet floral odors may be plesiomorphic with small modifications in certain species or may have been derived at least twice—once in *O. muelleri* and once in the common ancestor of *O. xylocarpa* and *O. caespitosa*.

The major points resulting from the cladistic analysis can be summarized as follows:

(1) The taxa analyzed can be divided into four distinct monophyletic groups: *O. muelleri*, *O. primiveris*, *O. xylocarpa*, and the *O. caespitosa* species group.

(2) Within the *O. caespitosa* species group there are two evolutionary lines that separated early in the evolutionary history of the group. *Oenothera caespitosa* subspp. *macroglottis*, *navajoensis*, and *marginata* and *O. harringtonii* constitute one group, and *O. caespitosa* subspp. *crinita* and *caespitosa*, *O. brandegeei*, and *O. cavernae* constitute the other. It is important to note that these two groups have a geographical basis with the first one eastern and the second western, with exceptions that *O. caespitosa* subspp. *marginata* and *caespitosa* have spread widely.

(3) Except for these two basic lines no two or more taxa are strongly linked by more than a few synapomorphies, and most that are linked are linked by only one. This may be due to a pattern of simultaneous divergence from a common ancestor and/or extensive parallelisms involving various kinds of simplification.

(4) The relationship of the pulvinate form of *Oenothera caespitosa* subsp. *crinita* to the other taxa is not clear. There are two conflicting placements of this form, neither of which is consistent with all of the data.

(5) Based on the characters used in the analysis, *Oenothera psammophila* and *O. caespitosa* subsp. *macroglottis* appears to have diverged from a common ancestor shared with subsp. *marginata*,

although some of their features, particularly of the capsule, suggest that hybridization with *O. caespitosa* subsp. *caespitosa* may have played a role in their origin.

Mode of Evolution and Origin of the *Oenothera caespitosa* Complex

Mode of Evolution

One of the most striking features of the *Oenothera caespitosa* group is that it has become adapted to a great variety of habitats and substrates. There are two basic ways populations have evolved in response to the pattern of cyclic but increasing aridity in western North America. Ecology, geography, cytology, breeding systems, and hybridization have had different but overlapping roles in each.

The first pattern is represented by the highly polymorphic *Oenothera caespitosa*. The primary feature of its pattern of evolution has been one of ecological diversification. Ecological shifts appear to have been of fundamental importance in isolating populations from one another. Not only has the origin of each subspecies involved significant ecological shifts, but there has also been considerable ecological diversification within some of the individual subspecies, such as *O. caespitosa* subspp. *marginata* and *crinita*. Ecological differentiation has not necessarily been accompanied by geographical separation. Judged from the four subspecies that are basically allopatric, however, considerable ecological changes have undoubtedly occurred as ancestral populations moved into new habitats in different geographical regions.

Despite the considerable degree of morphological and ecological divergence between the subspecies, they share a basic chromosome arrangement, and form fertile hybrids. Sometimes, there is a small degree of isolation locally in the seasonal timing of flowering such as that between *Oenothera caespitosa* subspp. *navajoensis* and *marginata* in a particular region but this is overcome by a considerable period of overlap. Although *O. caespitosa* subssp. *marginata* and *macroglottis* have adapted to pollination by the longer-tongued hawkmoths, *Sphinx* spp. and *Manduca quinquemaculata*, they are also pollinated by the shorter tongued *Hyles lineata* and are therefore not isolated from the subspecies with shorter floral tubes mainly pollinated by *Hyles*.

Fertile hybrids between the subspecies of *Oenothera caespitosa* have provided a rich source of new genotypes for selection to act on. Although a great number of these genotypes may not be well adapted to any environment, a small minority of them may represent better adaptations to certain environments than do any of those existing in either parent (Stebbins, 1969). This kind of system, where hybrids are fertile and barriers to hybridization are mainly external, occurs in most woody plants and many groups of herbaceous perennials (Raven, 1980; Grant, 1971). Hybridization has been a very important factor in the evolution of many well-known plant groups such as *Delphinium* (Lewis & Epling, 1959), *Diplacus* (Beeks, 1962), *Epilobium* (Raven & Raven, 1976), and *Iris* (Lenz, 1959). These groups have features similar to those described above for *Oenothera caespitosa*.

The second pattern of diversification involves even greater ecological and more fundamental morphological changes than that just described. Each of the other four species is very restricted geographically and edaphically. Each has undergone extreme specialization in relation to a narrow and extreme set of ecological circumstances. Adaptation to these habitats has involved much greater evolutionary changes than those found within *Oenothera caespitosa*. *Oenothera cavernae*, *O. brandegeei*, and *O. harringtonii* have switched from the perennial to the annual habit, while the fourth subspecies, *O. psammophila*, although perennial, has undergone a substantial adaptive shift to existence in a sterile lava and drifting sand habitat.

There also have been parallel changes in the breeding systems of these species. The desert annuals *Oenothera cavernae* and *O. brandegeei* have both lost self-incompatibility and become autogamous. Autogamy insures great success in seed set essential to these annuals as well as maintaining genotypes particularly well adapted to narrowly defined, marginal habitats through inbreeding. There have been less drastic changes in the breeding systems of *O. psammophila* and *O. harringtonii*. The former is pollinated not only by *Hyles* but noctuid moths as well, and *O. harringtonii* produces more flowers than does any other taxon in the group. These adaptations are viewed as ways to insure a large consistent supply of seeds.

There is good evidence that extensive chromosomal reorganization, genomic, and/or plastid differentiation has occurred in the origin of each of these edaphic specialists. This is in sharp

contrast to the pattern within *Oenothera caespitosa* where, other than the occasional tetraploids, there have been no significant changes of the latter kinds. For example, *Oenothera brandegeei,* differs from *O. caespitosa* by at least three reciprocal translocations.

Oenothera cavernae also may have undergone significant internal changes: F_1 hybrids with *O. caespitosa* are relatively slow-growing. Although *O. psammophila* and *O. harringtonii* produce fertile hybrids with *O. caespitosa* these hybrids are weak and often have slowly greening plastids indicating plastid differentiation, which is unknown within *O. caespitosa.*

ORIGIN OF THE *OENOTHERA CAESPITOSA* COMPLEX

The main evolutionary radiation of the tribe Onagreae has taken place chiefly in Madrean vegetation in western North America (Raven & Axelrod, 1978). The genus *Oenothera* is fairly typical in this respect. Two lines of evidence suggest the origin of *Oenothera* in the Madro-Tertiary vegetation in Mexico. Nearly all of the sections of the genus occur in Mexico, many associated with Madrean woodland or closely related vegetation types. In no other area can this diversity be matched. Secondly, within many sections of *Oenothera,* the more generalized species are found within Madrean vegetation in Mexico. For example, based on detailed studies of crossing relationships and morphology, the most generalized extant members of sect. *Oenothera* are the four species of subsect. *Emersonia,* three of which—*O. maysillesii* Munz, a related undescribed species, and *O. organensis* Munz—have very restricted, and presumably relictual, ranges in northern Mexico and southern New Mexico (Stubbe & Raven, 1979). All three are self-incompatible. The fourth species, *O. macrosceles,* is self-compatible and ranges more widely in northern Mexico, although it is not common. Likewise, most of the species and all of the more generalized bivalent-forming outcrossing members of the distantly related sect. *Hartmannia* also occur in and near Mexico in Madrean vegetation. Thus it appears likely that *Oenothera* originated and radiated in Madro-Tertiary vegetation during the spread and diversification of this vegetation in Neogene time and more recently.

The common ancestor of the *Oenothera caespitosa* group and related species (see Fig. 96) was also clearly associated directly with Madrean vegetation. *Oenothera muelleri,* the most generalized species of this lineage, has a disjunct range similar to that of the species of sect. *Oenothera* subsect. *Emersonia* to which it is related, occurring in Madrean woodland vegetation on several mountains in Nuevo León and as a morphologically distinctive population nearly 500 km north on Rincón de María, Coahuila.

Based on their occurrence in arid and semiarid vegetation types derived from the generalized Madro-Tertiary vegetation, the diversification of the remainder of this lineage, which includes *Oenothera primiveris, O. xylocarpa,* and the *O. caespitosa* group may well have been linked to the Pliocene spread of dry climate, resulting in part in western North America from the late Pliocene to Recent uplift of the Sierra Nevada. This period was a time when many plant groups radiated from the more southern, warm Madro-Tertiary vegetation into the cooler dryer climates that were rapidly spreading in western North America (Axelrod, 1958, 1979; Raven & Axelrod, 1978).

These three groups center in the Basin and Range region of western United States, and are now widely separated from the range of their extant sister-group, *Oenothera muelleri,* in eastern Mexico. The more generalized out-crossing and sometimes self-incompatible populations of *O. primiveris* are known from southern Nevada, Utah, and southern California, whereas other populations from Arizona to Texas of *O. primiveris* are autogamous and are clearly derived from the outcrossing race (Wagner, unpubl.). *Oenothera xylocarpa* is restricted to high elevations in and near the southern Sierra Nevada and Mount Rose in Nevada. Finally, the greatest diversity of elements from both lineages of the *O. caespitosa* group are found in southwestern Utah which includes both forms of *O. caespitosa* subsp. *crinita* and *O. cavernae* from one lineage and *O. caespitosa* subspp. *marginata* and *navajoensis* from the other. Thus, the *O. caespitosa* group probably originated in the Basin and Range region to the lee of the rising Sierra Nevada. It began to diversify and spread as oak-pinyon-juniper woodland assumed dominance throughout the region. The group has probably undergone the greatest part of its diversification during Quaternary time.

The only known fossils in the *Oenothera caespitosa* group are seeds collected during recent studies of packrat middens in the Grand Canyon.

Phillips (1977) found *O. cavernae* seeds about 11,500 years old in one midden near Rampart Cave, Mojave County, Arizona. Based on Phillip's reconstruction of the vegetation of the slope habitats, *O. cavernae* grew in essentially the same habit then as it does now. In fact, Phillips discusses several other species of these open rocky habitats such as *Crossosoma bigelovii* S. Wats. and several cacti with distributions that have remained essentially unaltered for the last 30,000 years. In contrast, most other taxa in the surrounding pinyon-juniper woodland retreated to high elevations or more mesic sites during the spreading aridity of the Holocene.

Systematic Treatment

Taxonomic History

The first species of this distinctive group of *Oenothera* species was collected by Thomas Nuttall in 1811 on a trip up the Missouri River. Nuttall described some of his collections, among them *O. caespitosa,* in what is now known as Fraser's Catalogue which according to Reveal (1968) was published in the summer of 1813. The catalogue, not much more than a list of species available at the Fraser Brothers Nursery in London, preceded Fredrick Pursh's description in early 1814 of this *Oenothera* in his comprehensive "Flora Americae Septentrionalis" as *O. scapigera.* Pursh based his name on a Lewis collection made in 1806 at Great Falls, Montana, the earliest known collection of the group.

Spach (1835a, 1835b) segregated *O. caespitosa* from *Oenothera* as a genus, *Pachylophus.* He did this as part of an overall generic splitting of the Onagraceae into small homogeneous groups of species in his "Histoire Naturelle des Végetaux" and later that same year in his "Monographia Onagrearum." This narrow generic concept was generally not accepted by others. For example, Endlicher (1840) treated ten of Spach's genera, including *Pachylophus,* as sections of *Oenothera.*

By 1840, two more names were added to the group, both based on Nuttall's collection and notes: *Oenothera marginata* (= *O. caespitosa* subsp. *marginata*) by W. J. Hooker and Arnott in "The Botany of Captain Beechey's Voyage" in January to March 1839 from a collection sent to them by William Fraser, with the epithet and notes sent by Nuttall in a letter and *O. montana* (here regarded as a pubescent form of *O. caespitosa* subsp. *caespitosa*), in Torrey and Gray's "Flora of North America" (1840). John Torrey (1852) suggested that these entities should be regarded as one species. Undoubtedly the plants collected on the Stansbury expedition influenced his comment as they were made from a population near the Great Salt Lake that contained intermediates between *O. caespitosa* subspp. *crinita* (not described until 1917) and *marginata.* In 1860, Durand formally reduced *Oenothera montana* to the status of a variety of *O. caespitosa.*

The first overall treatment of this group was that of Sereno Watson (1873). He did not recognize any subdivisions within *O. caespitosa.* The same treatment was followed by Raimann (1893) and by Small (1896) who recognized Spach's genus *Pachylophus.*

From 1890 to 1920 a number of species were described in the *O. caespitosa* group, primarily by Per Axel Rydberg (four species) and Aven Nelson (three). Rydberg's proposals included the entities recognized here as the remaining three subspecies of *O. caespitosa* (*crinita, macroglottis,* and *navajoensis*), and one of Nelson's species, *Pachylophus psammophilus,* is recognized as distinct.

In 1928 Phillip Munz initiated his useful series of revisionary studies of *Oenothera.* His paper on *Oenothera* subg. *Pachylophus* (1931b) made two important contributions: (1) he recognized the relatively close relationships, based primarily on seed characters, between the members of the *O. caespitosa* group and *O. primiveris, O. xylocarpa,* and *O. tubifera,* by including them in the subgenus; (2) he perceived that the *O. caespitosa* group was a diverse but closely related assemblage that he regarded as a single species. He subdivided this species into 11 varieties.

Only two other taxonomic papers that add new information to our understanding have been published since Munz's revision on this group. In 1941 Munz described the distinctive annual species *Oenothera cavernae,* but compared it with *O. primiveris,* to which it is not as closely allied as it is to *O. caespitosa.* The other paper, by Raven (1970), elevated *O. caespitosa* var. *brandegeei* to the rank of species because of its distinct features. He also effectively argued that, despite the overall resemblance of *O. brandegeei* to *O. cavernae,* they probably evolved independently from *O. caespitosa,* a view that we accept. He also reviewed subg. *Pachylophus,* considering *O. muelleri* and *O. macrosceles* in addition to those species included by Munz. *Oenothera macrosceles* has since been assigned to sect. *Oenothera*

subsect. *Emersonia* (Stubbe & Raven, 1979; Dietrich et al., 1985).

The present treatment differs substantially from that of Munz (1931b, 1965), who studied fewer than a tenth of the roughly 2,000 collections available to us and had very few fruiting specimens, which present an array of diagnostic features. Because of these problems, several of his entities (e.g., vars. *eximia, jonesii,* and *montana*) were artificial assemblages, based primarily on pubescence.

CRITERIA FOR ASSIGNMENT OF TAXONOMIC RANK

The primary purpose for grouping populations together into formal taxonomic categories is to provide a convenient means for communication about the organisms involved. Secondarily, the groupings are designed to express the presumed natural relationships of the populations. The important point is to construct an information-retrieval system with which we can meaningfully discuss the pattern of variation and the biology of the organisms as well as detect useful biogeographical and ecological patterns. There is a tendency to become preoccupied with detecting more or less discrete units in nature that can be given names, and much useful information can be lost in the process (Raven, 1977). The elucidation of evolutionary, genetic, or ecological properties is an independent endeavor that should not be directed toward the construction of classifications but rather at populations (Raven, 1977), the primary level at which evolution occurs. The classification system aids primarily in the communication of these investigations to others.

In delimiting species and subspecies in the *Oenothera caespitosa* group, discontinuities in the pattern of variation were emphasized as well as the degree of similarity between populations. Each taxon is based on the possession of a certain set of unique characters. These taxa are not considered to be units held together through interbreeding. Nevertheless, they are morphologically defined units in that they possess similar genetic, ecological, and physiological properties. Thus they do give us some predictive power.

Distinctive series of populations that intergrade have been treated here as subspecies. *Oenothera caespitosa* is composed of five such entities. *Oenothera caespitosa* subsp. *marginata* intergrades with the other four subspecies and subsp. *crinita* intergrades with subsp. *caespitosa*. There exists a range of intermediate situations ranging from sporadic hybrid individuals to large series of apparently stabilized hybrid derivatives that have their own geographical and sometimes ecological ranges. In contrast there are no known intermediates between the entities classified as species.

Individual plants were considered to be hybrids if they were intermediate in a few to many characters between the two putative parents, and if the parents were present in the general vicinity of the hybrid. All of these hybrids were essentially fully fertile. Hypotheses of hybrid origin for series of populations are more difficult to defend. Despite the lack of direct evidence in support of these hypotheses, there are several points that argue in favor of them as opposed to ones of primary divergence (these have been reviewed on p. 40).

Because of the complex variation pattern within some of the entities in this group it has been difficult to arrive at a coherent taxonomic treatment. We decided to be relatively conservative and treat five major population systems as subspecies of one polymorphic species. There is, however, a major philosophical difficulty with this approach. The fact that subspecies are logically subordinate to species implies that certain kinds of evolutionary changes are more significant than others. For example, is the switch to the annual habit and associated increase in the number of flowers of *O. harringtonii* more important than the extreme reduction of leaves, fruit, and flowers and the lower frequency of sexual reproduction characteristic of the pulvinate form of *O. caespitosa* subsp. *crinita*? Our decision was based on the fact that the entities fell into two distinctive groups based on overall patterns of variation: 1) the subspecies of *O. caespitosa,* which share many features such as habit and breeding system, are linked through a significant number of intermediate populations, and 2) the other four species, all of which are sharply distinct from *O. caespitosa* and each other. They have independently undergone major evolutionary changes in habit, breeding system, and ecological specialization.

TAXONOMY

KEY TO THE SPECIES

1. Petals 0.65–2.5 cm long; plants subacaulescent winter annuals; stigma surrounded by anthers at anthesis.
   2. Leaves with broad rounded lateral lobes,

the larger lobes usually alternating with smaller ones, and with reddish purple splotches and usually reddish tinged; plants usually with several short lateral branches; Grand Canyon region, S Nevada and S Utah ..... 4. *O. cavernae*

2'. Leaves with narrow, acute lateral lobes, the mature leaves neither with reddish purple splotches nor reddish tinged; plants strictly acaulescent; central Baja California ..... 5. *O. brandegeei*

1'. Petals (2–)2.5–6 cm long; plants perennial or if annual then with a stout erect stem 1–3 dm long; stigma well elevated above or outside the ring of stamens at anthesis.

3. Plants glabrous and with a resinous exudate, especially on the young parts; capsules often curved and often somewhat twisted, the valves with irregular wavy ridges; sand dunes in Fremont County, Idaho ..... 2. *O. psammophila*

3'. Plants pubescent or glabrous, but never with a resinous exudate; capsules never twisted, the valves tuberculate or ridged.

4. Plants coarse annuals, rarely overwintering for a second season, the stem densely leafy and erect; capsule valves with 5–8 conspicuous tubercles, 2–3 mm high; flowers 5 or more open at one time; SE Colorado ..... 3. *O. harringtonii*

4' Plants perennial, acaulescent or caulescent, the stems ascending to nearly erect; capsule valves with tubercles usually more than 8 or ridged, the tubercles or ridges 0.3–2 mm high; flowers 1–3(–10) open at one time; widespread ..... 1. *O. caespitosa*

1. Oenothera caespitosa Nutt. in Fraser's Cat. no. 53. 1813. TYPE: "Denuded, arid clay hills, banks of the Missouri River" somewhere between Big White River, Lyman Co., South Dakota and Fort Mandan, McLean Co., North Dakota, May–July 1811, *Nuttall* (lectotype, PH-0942394, photos BH, MO, POM; Munz, Amer. J. Bot. 18: 730. 1931). The specific locality where Nuttall collected the type was perhaps in Buffalo Co., South Dakota, somewhere between Chamberlain and a large ox-bow in the river near Lower Brule. This is based on an account from the journal of Bradbury (1904: 102) who in 1811 also travelled up the Missouri River with fur trappers and in this region "on May 29 . . . observed a number of large white flowers on the ground, belonging to a new species of *Oenothera*, having neither stem or scape, the flowers sitting immediately on the root." That *Oenothera* was clearly *O. caespitosa*; Sims, Bot. Mag. 39: pl. 1593. 1 Nov. 1813. Nutt., Gen. N. Amer. Pl. 1: 246. 1818. *Pachylophus caespitosa* (Nutt.) Raimann in Engl. & Prantl, Nat. Pflanzenfam. III, 7: 215. 1893. Britt. & Br., Ill. Fl. N. U.S. Ed. 2, 2: 603. fig. 3058. 1913. Rydb., Fl. Rocky Mts. 597. 1917. Tidestrom, Contr. U.S. Natl. Herb. 25: 380. 1925. Rydb., Fl. Plains N. Amer. 576. 1932. *Pachylophus nuttallii* Spach, Hist. Nat. Vég. Phan. 4: 365. 1835, nom. illeg., based on *Oenothera caespitosa* Nutt. Spach, Nouv. Ann. Mus. Hist. Nat. 4: 356. 1835 (as "*Pachylophis*").

Acaulescent or caulescent and loosely caespitose to pulvinate perennial herbs from a stout taproot, adventitious shoots sometimes produced from slender spreading lateral roots; stem 1 to many from a definite rosette, branching from near the base, these sometimes becoming buried, when above ground then ascending or rarely nearly erect, 1–4 dm long, hirsute (3 subspp.), villous (1 subsp.) with a mixture of minute glandular hairs or exclusively strigillose (1 subsp.), rarely glabrous in 2 subspp. Leaves in a rosette, gradually alternate, oblanceolate to rhombic or spatulate, rarely lanceolate or linear-oblanceolate, irregularly sinuate-dentate, pinnatifid, or subentire, (1.5–)2–25(–33) cm long, (0.3–)1–4 (–6.5) cm wide, acute to rounded at the apex, the teeth and lobes mostly acute but sometimes rounded, tapering to a winged petiole (0.2–)2–10(–14) cm long. Buds usually erect and lacking free sepal tips. Flowers with a moderate to strong sweet and somewhat rubbery odor, opening near sunset, generally 1–3(–10) open at once. Ovary reddish or brownish purple, sometimes paler, glandular pubescent and also hirsute, villous or strigillose, rarely glabrous. Floral tube yellowish green and sometimes tinged with red, (2.8–)4–14(–16.5) cm long. Sepals green or reddish usually with prominent reddish purple veins and in two subspp. also with reddish purple splotches, (1.5–)2–4.5(–5.4) cm long, (0.2–)0.5–1.1 cm wide. Petals opening to an approximately horizontal plane (or nearly vertical in one subspp.), (1.6–)2–4.5(–5.6) cm long, (1.8–)2.5–6.3(–7) cm wide. Staminal filaments (6–)12–28(–35) mm long; anthers (6–)9–17(–20) mm long. Style (4.5–)4–17 (–18.5) cm long; stigma elevated above or outside of the ring of stamens, (2.5–)4–8(–12) mm long. Capsule cylindrical to lanceoloid or ellipsoid, straight to falcate or sigmoid, nearly symmetrical or strongly asymmetrical at the base, (1–)1.5–5(–6.8) cm long, tapering to a sterile beak 6–8 mm long, the free tips 0.2–4 mm long, erect

to recurved, the valves with rows of distinct tubercles to sinuate or nearly smooth ridges along the margin, dehiscing ⅓–⅞ their length, sessile to long pedicellate. Seeds (20–)30–100(–170) per capsule, arranged in 1 or 2 rows per locule; embryo portion papillose, reticulate or irregularly roughened (1 subsp.), constituting ⅕–⅔ of seed volume; seed-collar sealed by a thin membrane, this flat or depressed into the raphial cavity, when depressed often splitting and becoming separated from the seed-collar. Self-incompatible. Gametic chromosome numbers, $n = 7, 14$.

Distribution. Local and colonial, rarely abundant in open sites such as cracks in rocks, rocky slopes, alluvial deposits, arroyo banks, gumbo, slopes and flats around harvester ant mounds and rodent holes, in vegetation types ranging from grassland margins of desert scrub, pinyon-juniper woodland, or Arizona chaparral to montane conifer forests, rarely at timberline with *Pinus longaeva* from eastern Washington and Oregon to southern Alberta and Saskatchewan south to North and South Dakota, west of the Missouri River south through all but extreme eastern Colorado and New Mexico to the Guadalupe Mountains in Trans-Pecos Texas and Carretas in northwestern Chihuahua west to the Inyo region in southeastern California, 450–3,350 m. Flowering from mid-March to July, rarely later.

Oenothera caespitosa as delimited here consists of five broadly defined variable subspecies, *crinita, caespitosa, navajoensis, macroglottis,* and *marginata.* Each might be accorded specific rank were it not for the fact that intermediates are known between five pair combinations of the subspecies. The sequence of the subspecies in this treatment reflect relationships of one to the other.

KEY TO THE SUBSPECIES OF *O. CAESPITOSA*

1. Plants conspicuously pubescent, rarely appearing glabrous (under magnification pubescent with minute glandular hairs).
   2. Plants with short (less than 0.5 mm) appressed to somewhat spreading hairs, minute glandular hairs absent (except sometimes in plants from Oregon or N Nevada); capsule asymmetrical at the base, falcate or sigmoid; petals fading rose purple; Washington to N Nevada, E to North Dakota, Nebraska, and N Colorado ..... 1b. subsp. *caespitosa*
   2′. Plants hirsute or villous of if the hairs somewhat appressed (N Nevada and NE Utah) then some of them at least 1 mm long, with a mixture of minute glandular hairs, sometimes only glandular; capsule various.
      3. Plants many branched from the base, forming densely pulvinate mats; petals fading rose; seed-collar sinuate distally; central Nevada, W Utah, and Inyo region of California ... 1a. subsp. *crinita*
      3′. Plants simple to several branched, caespitose, not forming pulvinate mats; petals fading rose purple or pink; seed-collar various.
         4. Petals fading rose purple, sometimes deep pink; capsule ellipsoid to lance-ellipsoid, falcate, and conspicuously asymmetrical at the base, the pedicels ca. 1 mm long or less; seed collar sinuate throughout and often ribbed externally, the membrane depressed and splitting at maturity; Nevada, W Utah, and Inyo region of California ..... 1a. subsp. *crinita*
         4′. Petals fading pink rarely slightly darker; capsule oblong-lanceoloid to cylindrical, straight or somewhat curved and slightly asymmetrical at the base, the pedicels mostly 2–50 mm long; seed-collar not conspicuously sinuate, sometimes somewhat so distally, the membrane neither depressed nor splitting at maturity.
            5. Capsules oblong-lanceoloid abruptly contracted to a sterile beak, the dehiscing valves erect or incurved; floral tubes 3.5–6(–7) cm long, often recurved when young; plants shaggy villous, sometimes densely so; Colorado Plateau ..... 1c. subsp. *navajoensis*
            5′. Capsules cylindrical to lance-cylindrical tapering gradually to a sterile beak, the dehiscing valves spreading; floral tubes (5–)7–16 cm long, erect; plants hirsute.
               6. Capsule somewhat curved, the valves with smooth to irregular ridges; leaves mostly oblanceolate to spatulate, the margins dentate; mountains of Colorado, SE Wyoming, N New Mexico, and SE Utah ..... 1d. subsp. *macroglottis*
               6′. Capsule straight, the valves with tuberculate ridges or rows of nearly distinct tubercles; leaves oblanceolate to lanceolate or elliptic; typically pinnately lobed; widespread ..... 1e. subsp. *marginata*

1′. Plants glabrous.
   7. Floral tubes (2.8–)3.5–7.5(–8.5) cm long; petals fading rose purple; capsule falcate, distinctly asymmetrical at the base; the valves tuberculate; Washington to N Nevada, E to North Dakota and SW Nebraska and N Colorado ..... 1b. subsp. *caespitosa*
   7′. Floral tubes (4.5–)7.5–11(–15.3) cm long; petals fading pink or rarely rose; capsule somewhat curved and slightly asymmetrical at the base, the valves with smooth to irregular ridges; Colorado, SE Wyoming, N New Mexico, and SE Utah ..... 1d. subsp. *macroglottis*

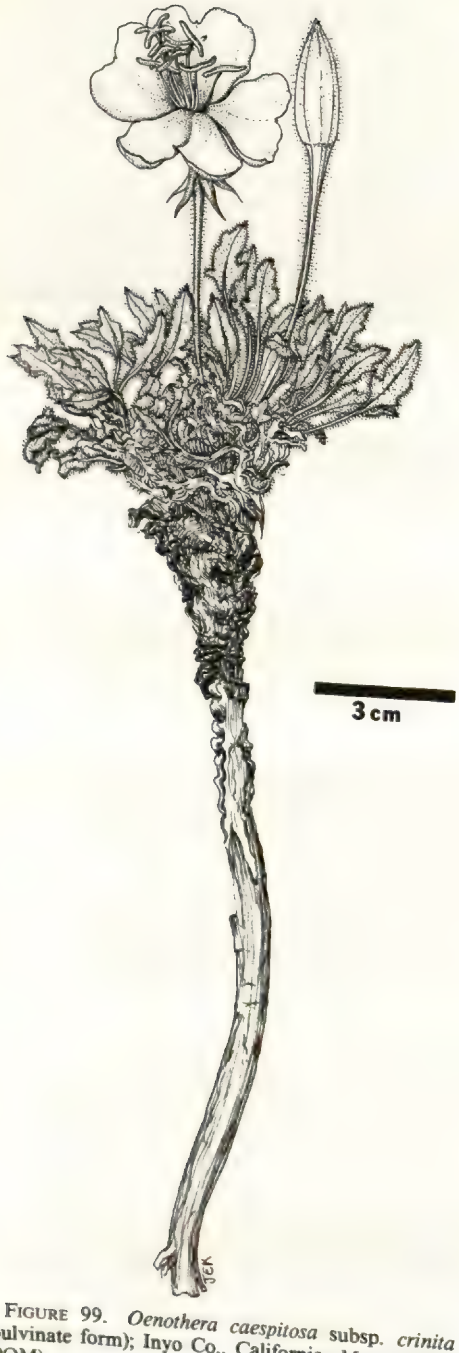


FIGURE 99. *Oenothera caespitosa* subsp. *crinita* (pulvinate form); Inyo Co., California, *Munz 14779* (POM).

1a. Oenothera caespitosa Nutt. subsp. **crinita** (Rydb.) Munz, N. Amer. Fl., Ser. II, 5: 100. 1965. Munz, Fl. S. Calif. 613. 1974. Beatley, Vasc. Pl. Nev. Test Site & Cent. S. Nev. 209. 1976. *Pachylophus crinitus* Rydb., Fl. Rocky Mts. 598, 1064. 1917. TYPE: Said to be from "Rabbit Valley" which is between Loa and Bicknell, 2,150 m, Wayne Co., Utah, 6 Aug. 1875, *Ward 526* (holotype, US-140110 pro parte; photos MO, UTC; isotypes, GH, PH). This locality and the localities attributed to *Ward 16* [a mixture of *O. caespitosa* subsp. *navajoensis* (PH, US) and subsp. *marginata* (GH)] and *Ward 167* (subsp. *crinita*) which are also mounted on the same sheet with *Ward 526* are N or E of any known localities of subsp. *crinita*. The type is a close match for plants 130 km S of Rabbit Valley in the Red Canyon area, Garfield County, Utah, and is likely from that area. We could not determine whether Ward collected any farther S or W of the Aquarius Plateau (Ewan, 1950: 331) some 46 km away from Red Canyon. Others have thought Ward's labels to be confused (cf. Pennell, 1920: 339). To date there has not been a compilation of Ward's itineraries and the plants collected. Tidestrom, Contr. U.S. Natl. Herb. 25: 380. 1925. *Oenothera caespitosa* Nutt. var. *crinita* (Rydb.) Munz, Amer. J. Bot. 18: 731. 1931. Clokey, Univ. Calif. Publ. Bot. 24: 158. 1951. Munz, Calif. Fl. 950. 1959. Figure 99.

Oenothera caespitosa Nutt. var. *jonesii* Munz, Amer. J. Bot. 18: 731. 1931. TYPE: Fish Springs, N end of Fish Springs Range, Juab Co., Utah, 4 June 1891, *Jones* (holotype, POM-38813, photo MO). According to his journal (Jones, 1965) he was at the Fish Springs in Juab Co., Utah not the one in Grand Co., Utah as believed by Munz (1931b). *Oenothera caespitosa* Nutt. subsp. *jonesii* (Munz), N. Amer. Fl., Ser. II, 5: 100. 1965.

Oenothera caespitosa var. *marginata* sensu Munz, Amer. J. Bot. 18: 733. 1931, pro parte; Calif. Fl. 949. 1959, pro parte; Fl. S. Calif. 613. 1974, pro parte, non (Nutt. ex Hook.) Munz.

Oenothera caespitosa var. *montana* sensu Abrams, Illus. Fl. Pac. States III: 195. fig. 3414. 1951, pro parte, non (Nutt.) Durand.

Acaulescent or caulescent and loosely caespitose to pulvinate perennial herb from a stout woody taproot, adventitious shoots sometimes produced from slender roots; stems, if present, 6–14 cm long, simple to many-branched from near the base with 6–10 cm buried so that the

rosette is near the ground level; plants producing dense pulvinate mats 0.5–5 dm across. Leaves grayish green, rarely green, densely hirsute, the hairs 0.5–1.5 mm long, typically stiffly erect or spreading, sparsely mixed with minute glandular hairs 0.1–0.2 mm long, pubescence of larger leaves often less dense and more restricted to the lower surface or along the margin and major veins, oblanceolate to linear-oblanceolate, rarely obovate, 1.7–10(–18) cm long, (0.3–)0.5–2.5(–3.4) cm wide, acute to rounded at the apex, subentire, sinuate or dentate to pinnatifid, the teeth triangular, rarely rounded, mostly 0.5–4 mm high, the larger lobes 4–11 mm high, tapering to a petiole (0.2–)3–5(–8) cm long. Buds erect. Flowers 1–2(–4) per stem opening per day. Ovary densely or rarely sparsely hirsute, moderately mixed with minute glandular hairs, 6–12(–15) mm long, sessile or on a short pedicel ca. 1 mm long. Floral tube (2.8–)3.5–7.5(up to 8.5 at low elevations of Inyo County, California) cm long, 1–1.5(–1.8) mm diam. medially, flaring to 4–8 (–9) mm at the mouth, densely hirsute mixed with minute glandular hairs to subglabrous. Sepals green, the veins infused with reddish purple pigment sometimes also with reddish purple splotches, (1.5–)1.8–2.5(–2.7) cm long, (3–)4–5 mm wide, pubescence the same as the floral tubes, often more densely hirsute along the margins and midvein. Petals fading rose or a deep rose purple, (1.6–)2–3(–3.5) cm long, (1.8–)2.5–4(–4.5) cm wide, the notch 5–8(–10) mm deep, subglabrous. Staminal filaments (6–)10–17(–20) mm long; anthers 6–8(–10) mm long. Style (4.5–)6–9(–10.5) cm long; stigma lobes 2.5–7 mm long. Capsules 0–7(–12) maturing per stem, elliptic-ovoid to lanceoloid, usually falcate or stigmoid especially when young, also somewhat flattened, asymmetrical and cuneate at the base, rarely nearly symmetrical in high elevation populations, 1–3.1 (–3.4) cm long, rounded in cross-section, 4–9 mm diam., gradually tapering to a sterile beak 3–5(–8) mm long, the free tips less than 1 mm long, recurved, hirsute and glandular pubescent, sometimes becoming glabrate in age, the margins of the valves with 8–15 tubercles or these coalesced into a sinuate ridge, 0.3–1.5 mm high, ca. 1.5 mm apart, the cross-veins prominent near the ridge, dehiscing ⅓–½ their length, the valves spreading, sessile or on a short somewhat flattened pedicel ca. 1 mm long. Seeds (20–)30–90 per capsule in two distinct rows or nearly so, the raphe parallel or oblique to the plane of the capsular axis, obovoid, oblong or roughly triangular, often curved, brown to dark reddish brown or nearly black, the collar often lighter, 2.9–3.5 mm long, 1.1–2 mm wide, 1.2–1.5 mm high; embryo portion constituting ½–⅔ of the seed volume, the surface papillose, reticulate or very minutely roughened, appearing longitudinally striate under low magnification; seed-collar nearly triangular, the membrane depressed and often splitting and becoming separated from the collar at maturity, the margin pinnate, sometimes only distally, the surface often ribbed, the ribs forming partial or complete vertical partitions in the collar. Gametic chromosome numbers, $n = 7, 14$.

Distribution (Fig. 100). On open sites of compacted, rarely loose soils derived from dolomite, limestone, tufa, or marble; exposed knolls, gravelly benches, steep slopes, scree, rocky mesas, or along rocky arroyos from mountain summits in alpine or subalpine communities with *Pinus longaeva* and *P. flexilis* James or pinyon-juniper woodland to Great Basin or Mojave Desert shrub communities dominated by *Artemisia* spp., *Atriplex confertifolia* (Torrey & Frémont) S. Wats., *Coleogyne, Lycium,* and *Hilaria,* from Modoc County, California nearly throughout Nevada to eastern Utah east of the Wasatch Range south to Mohave County, Arizona and west to the Inyo Region of southeastern California, 1,150–3,370 m. Flowering mid-April to early July.

Representative specimens examined. (* refers to collections of the pulvinate form. Unmarked collections are the common form.) UNITED STATES. ARIZONA: Mohave Co., 45 mi. S of St. George Rd. to Mt. Dellenbaugh, *Holland 1273* (UNLV). CALIFORNIA: Inyo Co., Harrisburg Flat S to Wild Rose Station, *Gregory 400* (CAS, DS, GH, UC); Dante's View, *Hitchcock 12336* (CU, DS, F, MO, MONTU, NA, POM, UC); Panamint Mts., Telescope Peak, *Munz 14779** (CAS, GH, MO, POM). Modoc Co., Likely, 1920, *Manning s.n.* (JEPS). Mono Co., Convict Lake, 1938, *Noldeke s.n.** (CAS). San Bernardino Co., Cushenbury Spring, *Parish & Parish 1307* (BM, DS, G, MO); Clark Mt., N side of main peak, *Wolf 7598** (DS, RSA). NEVADA: Clark Co., Charleston Peak, *Clokey 5539** (BH, CAS, DS, F, LA, ND, NY, RM, RSA, UC, UTC, WS); Ranger Mts., N of Mercury, *Raven 18915* (DS); Charleston Mts., South Loop Trail, ca. 1 mi. SE of Echo Cliffs, *Wagner 4494** (MO). Elko Co., 2 mi. SE of Elko, *Marineau 73* (BRY, NESH, RENO). Esmeralda Co., Magruder Mt., Silver Peak Range, *Maguire & Holmgren 25642** (GH, NY, UC, US, UTC); Candelaria, *Shockley 206* (DS, GH, UC). Eureka Co., 18 mi. W of Eureka, *Ripley & Barneby 6230** (CAS, NY). Humboldt Co., Virgin Valley, Sheldon Nat'l. Wildlife Refuge, *Tiehm & Rogers 4192* (MO, RENO). Lander Co., Bunker Hill, Toiyabe Reservoir, *Kennedy 4098** (DS, E, G, MO, PH, RM, UC). Lincoln Co., S end of Buried Hills, Frenchman Flat, *Beatley & Bostick 4217* (NTS); Eagle

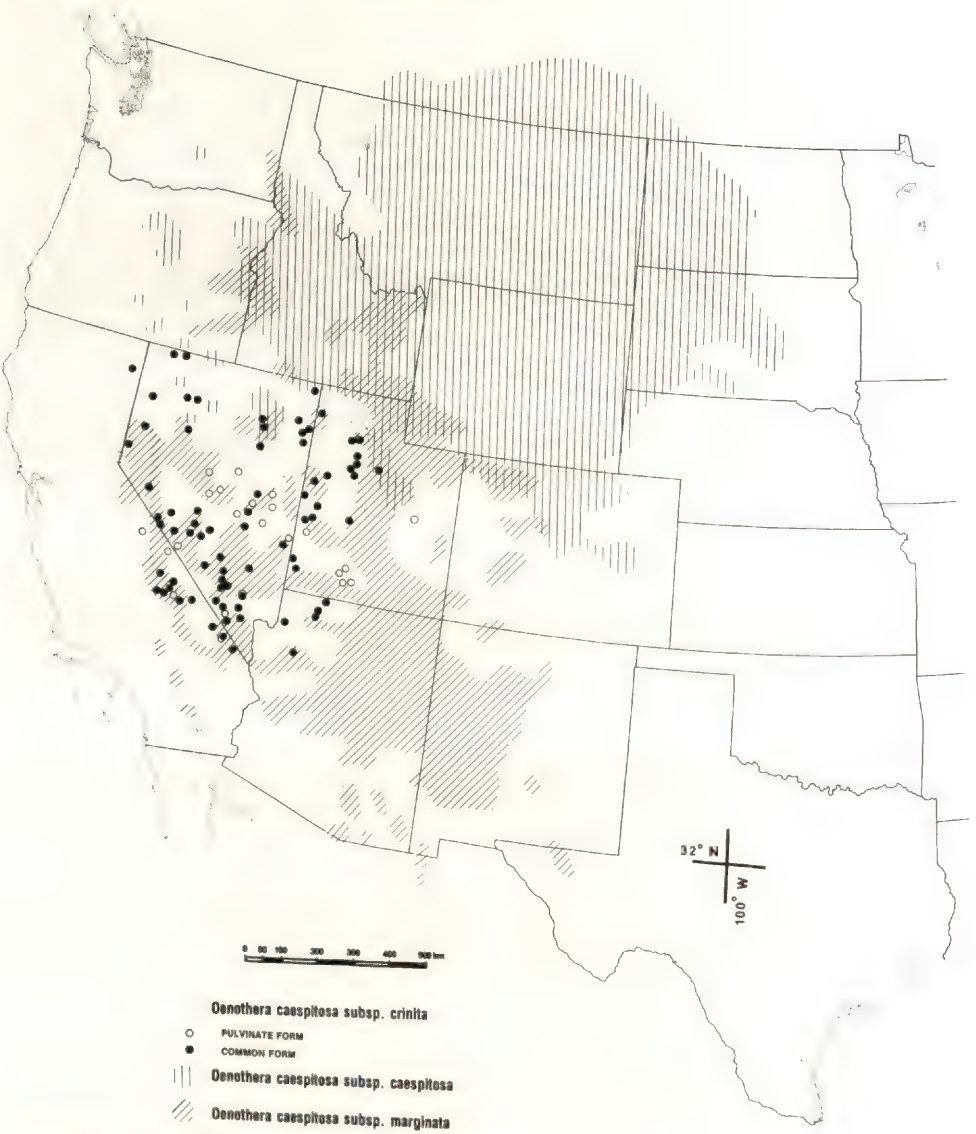


FIGURE 100. Distribution of *Oenothera caespitosa* subsp. *crinita* relative to subspp. *caespitosa* and *marginata* (shaded).

Valley, 3.4 mi. N of campground (T2N, R69E, Sec. 12), *Harrison & Thorne 1152** (BRY). Mineral Co., Wassuk Range, Cory Canyon, *Alexander & Kellogg 4442* (DS, UC). Nye Co., W Cactus Flat, E slope of Cactus Range, *Beatley 9291* (NTS, RSA); Monitor Valley, Dinah's Punch Bowl, *Maguire & Holmgren 25757** (GH, NY, UC, UTC). Pershing Co., Goldsprings, near Rochester, 1935, *Train s.n.* (US). Washoe Co., Virginia Mts., E side of Honey Lake Valley, *Tiehm 5929* (MO). White Pine Co., 7 mi. N of Ely, *Moore & Franklin 121* (NA, NY, POM); Egan Range, 0.5 mi. W of Ely on Hwy. 50, *Tiehm, Williams & Birdsey 5308** (BRY, MO). UTAH: Beaver Co., Needle Mts., S of Cargar Spar Mine, *Peck 38* (UT); 1 mi. N of Lone Fence, Red Hills, *Stahmann & Hutchings 58** (UT). Box Elder Co., 20 mi. N of Lucin, *Maguire 21521* (BRY, NY, UTC). Emery Co., Red Plateau, SW of Woodside, *Ripley & Barneby 8679** (CAS, NY). Garfield Co., 3.6 mi. S of Hatch, Hwy. 89, *Wagner 4505** (MO). Iron Co., Hwy. 56 at Utah-Nevada line, *Conrad, Morris & Kenny 6708*, pro parte (UMO). Juab Co., 18 mi. E of Troutcreek, Honeycombs, *Maguire & Becraft 2702* (CU, UTC).

Kane Co., Utah Hwy. 54 jct. at Cannonville, *Reveal, Gentry & Davidse 798** (ARIZ, BRY, CAS, COLO, CU, DS, GH, ID, KANU, NA, NY, OSC, UC, UTC). Millard Co., Pine Valley, Warm Point (T25S, R18W, Sec. 26), *Welsh & Atwood 9682* (BRY). Tooele Co., Simpson Mts., *Maguire & Holmgren 21840* (BH, GH, NA, NY, UTC). Utah Co., N of Enterprise, *Hall EN21* (F, UT).

Intermediates between *Oenothera caespitosa* subsp. *crinita* and subsp. *caespitosa*:

NEVADA: Elko Co., 40 mi. E of Wells along Hwy. 40, *Gallian & Leake 755, 769* (UMO); Delano Mts., 2 mi. N of Crittenden Ranch, *Train 3692* (NA); 22 mi. S of Wendover, Hwy. 50, *Train 3822* (NA). Lander Co., 10 mi. E of Battle Mt., *Eastwood & Howell 161a* (CAS, POM).

Intermediates between *Oenothera caespitosa* subsp. *crinita* and subsp. *marginata*:

CALIFORNIA: Inyo Co., Panamint Mts., *Coville & Funston 535* (DS, GH, MO, NY, PH); Harrisburg Flat, S for 5 mi., *Gregory 400* (SD, RSA); Panamint Mts., Pleasant Canyon, *Hall & Chandler 6959* (POM, RM, UC); Panamint Mts., Johnson Canyon, *Jepson 19772* (JEPS); Darwin, 1897, *Jones s.n.*, pro parte (POM); Argus Mts., Shepherds Canyon, *Keller 126* (SD); Panamint Mts., Mahogany Flats, *Woglum 2812* (RSA). San Bernardino Co., Panamint Mts., Wild Rose Canyon, *Parish 9995* (DS, MO, UC); Clark Mts., Cactus Canyon, *Prigge & Prigge 647* (NY). NEVADA: Clark Co., 13 mi. W of Jean on rd. to Kingston, *Gregory 378* (RSA). Esmeralda Co., Palmetto Range, *Purpus 5882*, pro parte (PH). Nye Co., Grapevine Mts., Titus Canyon, *Welsh, Atwood & Mathews 4627* (BRY). UTAH: Beaver Co., 29.4 mi. NW of Lund, roadside (one plant), *Wagner 4502* (MO). Iron Co., Utah-Nevada State line, Hwy. 56, *Conrad et al. 6708*, pro parte (UMO).

Oenothera caespitosa subsp. *crinita* is by far the most polymorphic subspecies of *O. caespitosa*; it is also the least understood. It is characterized by a combination of a usually dense hirsute covering of hairs over most of the plant, typically sparsely mixed with minute glandular hairs; rose to rose purple color of the faded petals; floral tubes 2–7 cm long; capsules falcate or sigmoid, elliptic-lanceoloid and often somewhat flattened with a strongly asymmetrical base; and seed-collar with a sinuate margin and ribbed internally, the ribbing often distinctly visible externally. Because most of the vegetative and floral tube features are continuously variable and we lack detailed information on the distribution of capsule and seed features in many populations, it seems best to unite all plants with the features listed above into one polymorphic subspecies. A finer taxonomic subdivision at this time would suggest a greater degree of understanding of the relationships of these populations than we presently have. To compound the problem many foothill and valley populations of

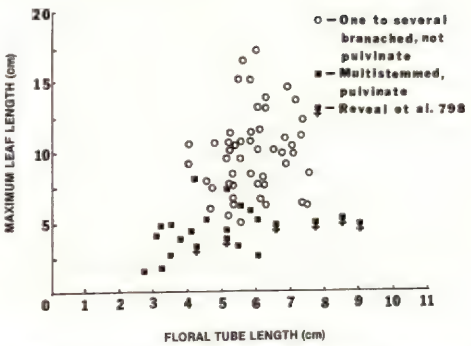


FIGURE 101. Morphological comparison of the two forms of *Oenothera caespitosa* subsp. *crinita*.

subsp. *crinita* intergrade extensively with both subsp. *marginata* and the more closely related subsp. *caespitosa*.

Within subsp. *crinita* there are two series of populations that appear to intergrade (Fig. 101):

1. A many-branched pulvinate race, which may form mats to 50 cm in diam., occurs at high elevations on rocky limestone sites or at lower elevations on extreme chalky, white limestone and dolomite substrates or sometimes scree slopes. In addition to the low mat-forming habit it also differs from the common form in that its leaves are 2–7 cm long, floral tubes 2.5–6 cm long and the petals fade to a rose color. Munz's (1931b, 1965) concept of subsp. *crinita* was primarily confined to plants of this race.

2. The more common form occurs at low to mid-elevations on rocky slopes, tallus, or along arroyos. It is much less compact and is acaulescent with one to several clustered rosettes or rarely more elongate with short congested stems. The leaves are 8–16 cm long, floral tubes 4.5–7.5 cm long, petals that fade rose purple, and seed-collars internally ribbed, the ribs usually visible externally.

This form is found in pinyon-juniper woodlands to Great Basin or Mojave Desert scrub. The common form also grows on limestone and dolomite, but, unlike the pulvinate form, it does not seem to be restricted to it. Munz included many of these plants in *Oenothera caespitosa* subsp. *marginata* (1931b, 1965), probably because of the rather continuous intergradation between them and subsp. *marginata* in certain areas. The possession by both races of similar capsule features and internal ribbing of the seed-collars clearly shows that they are more closely related to each other than either is to *O. caespitosa* subsp.

marginata, which has smooth-walled seed-collars. Munz also included some plants of the common form of *O. caespitosa* subsp. *crinita,* particularly from Utah, in his artificial and heterogeneous subsp. *montana.*

One tetraploid plant, with several quadrivalents at meiotic metaphase I, was obtained by Goeken (1968) in a population from Inyo County, California. Tetraploid plants, however, could not be found again when other individuals were grown from this collection by Stockhouse (1973), and they are probably only of sporadic occurrence in some populations of this subspecies. No cytological information is available concerning the pulvinate form of this subspecies.

The pulvinate race is in general morphologically relatively uniform, which is undoubtedly related to the fact that it is the product of an extreme reduction series. Several features, however, are somewhat variable. The leaves are quite variable, but size and degree of lobing exhibit no apparent geographical pattern. This variation is presumably related to severity of site conditions. On the other hand, variation in seed coat morphology is apparently geographical. The high-elevation plants examined thus far all have an irregularly roughened surface with individual epidermal cells on the surface not distinguishable, whereas the seeds of low-elevation plants are papillose where each papillae is one epidermal cell. Unfortunately, the high-elevation race produces very few capsules and we therefore have been unable to determine if this difference is consistent.

In general, the floral tubes of the pulvinate race are rather uniform in length. The tubes within most populations typically range from 3 to 5.5 cm. One population from Kane County, Utah (*Reveal et al. 798*), however, is exceedingly variable in this feature; the tubes range from 4.3 to 9.1 cm long, with a mean length of 6.2 cm. The mean tube length is longer than the longest tubes in most populations of this subspecies (Fig. 101). The other features of this population are well within the normal range, but the highly diagnostic capsule and seed features are unknown. Either this population has been derived following hybridization with *Oenothera caespitosa* subsp. *marginata* in the past or there has been strong local selection for longer tube length.

The common form is considerably more variable than the pulvinate form, and much of the variation has a geographical basis. The different morphological forms grade rather smoothly into one another. Moreover, the fact that the common form of *Oenothera caespitosa* subsp. *crinita* intergrades with both subsp. *marginata* and subsp. *caespitosa* evidently enhances its variability. The following variations seem noteworthy:

1. *Habit.* Plants range from those that possess a single rosette to others that have four or five clustered rosettes. The latter approach the pulvinate form and are especially frequent in the southern portion of the range. In the north, the habit of plants with multiple rosettes tends to be more open.

2. *Leaves.* Sometimes they vary from pinnatifid to pinnately-lobed in the same population (e.g., *Raven 18915,* Clark County, Nevada), but more often they are coarsely pinnate and may or may not become lobed toward the base. Early season leaves tend to be broader and fewer lobed (e.g., *Tiehm 5900,* Washoe County, Nevada).

3. *Pubescence.* Hirsute pubescence is typically rather dense on leaf surfaces but sometimes they are more restricted to the margins and veins, the blades then being rather green. In plants from Utah, the pubescence is finer than usual and sometimes somewhat curly; in northern Nevada, the hairs are shorter than usual (0.6–1 mm), coarser, and somewhat appressed (e.g., *Tiehm & Rogers 4192,* Humboldt County). The latter form may have been derived following hybridization with *Oenothera caespitosa* subsp. *caespitosa.*

4. *Seeds.* When the extremes are considered, two quite different seed forms are apparent. In the south, especially Clark County, Nevada, the seeds are robust, often 3–3.5 mm long, with an enlarged distal end, often making the overall seed shape nearly triangular in outline, with a papillose surface and prominent external ribbing. At the opposite extreme are oblong seeds 2.5–3 mm long with a reticulate surface which are not strongly ribbed and lack a collar membrane. Most populations have intermediate seeds: oblong to oblong-obovoid, strongly ribbed, papillose, and with a depressed collar membrane. The differences between papillose and reticulate seeds may be simple genetically and it is at least partly related to pressure from adjacent seeds during development. In capsules with a full complement of seeds the abaxial surface is sometimes partly reticulate where it touches adjacent seeds, the lateral surfaces papillose. The seeds of some populations from Millard County, Utah, however, are entirely reticulate without apparent pressure.

1b. Oenothera caespitosa Nutt. subsp. **caespitosa**; Munz, N. Amer. Fl., Ser. II, 5: 100. 1965. Van Bruggen, Vasc. Pl. S. Dak. 327.

FIGURE 102. *Oenothera caespitosa* subsp. *caespitosa*; Teton Co., Montana, *Gregory 457* (GH).

1967. Weber, Rocky Mt. Fl. 247. fig. 167. 1967. Dorn, Fl. Black Hills, N. Dak. 239. 1977; Man. Vasc. Pl. Wyo. II: 1005. 1977, pro parte. *Oenothera caespitosa* Nutt. var. *typica* Munz, Amer. J. Bot. 18: 730. 1931. *Oenothera caespitosa* Nutt. var. *caespitosa*; Stevens, Hanb. N. Dak. Pl. 215. 1950. Harrington, Man. Pl. Colo. 396. 1954. Hitchcock et al., Vasc. Pl. Pac. Northw. 495. 1961. Hitchcock & Cronquist, Fl. Pac. Northw. 310. 1973. Figure 102.

Oenothera scapigera Pursh, Fl. Amer. Sept. 1: 263. 1814. Although a few copies of Pursh's flora were available in late 1813 (Stafleu, 1967: 369), it was not generally available until 1814; thus the name *Oenothera caespitosa* Nutt. was clearly published earlier. TYPE: "Falls of the Missouri River," Cascade Co., Montana, 17 July 1806, *Lewis s.n.* (lectotype here designated, PH, photo MO; isolectotype, PH).

Oenothera montana Nutt. in Torr. & A. Gray, Fl. N. Amer. 1: 500. 1840. TYPE: "Plains of the North Platte River between Fort Laramie and Independence Rock," Platte, Converse, or Natrona Co., Wyoming, 1–8 June 1834, *Nuttall s.n.* [lectotype, BM, photo MO; isolectotypes, NY, PH; chosen by Munz without seeing material (1931b: 732)]. Locality reconstructed with aid of McKelvey (1955: 595). *Oenothera caespitosa* Nutt. var. *montana* (Nutt.) Durand, Trans. Amer. Philos. Soc., Ser. II, 11: 164. 1860. Munz, Amer. J. Bot. 18: 732. 1931, pro parte. Abrams, Illus. Fl. Pac. States III: 195. 1951, pro parte. Davis, Fl. Id. 497. 1952. Hitchcock et al., Vasc. Pl. Pac. Northw. 495. 1961. Peck, Man. High. Pl. Ore. Ed. 2, 544. 1961. Hitchcock & Cronquist. Fl. Pac. Northw. 310. 1973, pro parte. *Pachylophus montanus* (Nutt.) A. Nels., Bull. Torrey Bot. Club 26: 128. 1899. Rydb., Fl. Rocky Mts. 598. 1922. Tidestrom, Contr. U.S. Natl. Herb. 25: 380. 1925. Rydb., Fl. Plains N. Amer. 576. fig. 397. 1932. *Oenothera caespitosa* Nutt. subsp. *montana* (Nutt.) Munz, N. Amer. Fl., Ser. II, 5: 101. 1965. Van Bruggen, Vasc. Pl. S. Dak. 327. 1976.

Oenothera marginata Nutt. ex Hook. & Arn. var. *purpurea* S. Wats., Bot. King's Expl. 108. 1871. TYPE: "East Humboldt Mountains" (Ruby Mountains according to Cronquist et al., 1972: 54), 2,400 m, Elko Co., Nevada, July 1868, *Watson 412* [lectotype, GH, photos MO, UTC; isolectotypes, NY, YU; Munz (1931b: 730)]. *Oenothera caespitosa* Nutt. var. *purpurea* (S. Wats.) Munz, Amer. J.

Bot. 18: 730. 1931. Abrams, Illus. Fl. Pac. States III: 195. 1951. Davis, Fl. Id. 498. 1952. Hitchcock et al., Vasc. Pl. Pac. Northw. 495. 1961. Peck, Man. High. Pl. Ore. Ed. 2, 544. 1961. Hitchcock & Cronquist, Fl. Pac. Northw. 310. 1973. *Oenothera caespitosa* Nutt. subsp. *purpurea* (S. Wats.) Munz, N. Amer. Fl., Ser. II, 5: 100. 1965.

Pachylophus glaber ("*glabra*") A. Nels., Bull. Torrey Bot. Club 31: 242. 1904. TYPE: "Platte River bottoms, near Badger" (Sec. 16, T27N, R67W), 1 mi. SW Wendover, Platte Co., Wyoming, 1 June 1901, *Nelson 8340a* (holotype, RM-65439, photo MO; isotype, NMC). Locality reconstructed with aid of Ronald Hartman and Robert Dorn (pers. comm.).

Pachylophus canescens Piper, Contr. U.S. Natl. Herb. 11: 409. 1906. TYPE: Sentinel Bluffs, Kittitas Co., Washington, 14 July 1903, *Cotton 1345* (holotype, US-528807, photo MO; isotypes, GH, POM, US, photo MO). Rydb., Fl. Rocky Mts. 598. 1922. Tidestrom, Contr. U.S. Natl. Herb. 25: 380. 1925. Rydb., Fl. Plains N. Amer. 576. 1932.

Pachylophus eximius sensu Rydb., Fl. Rocky Mts. 598. 1922, pro parte (as to plants from South Dakota); Fl. Plains N. Amer. 576. 1932, pro parte, non (A. Gray) Woot. & Standl.

Acaulescent or caulescent and loosely caespitose perennial herb from a stout fleshy or somewhat woody taproot, adventitious shoots sometimes produced from spreading lateral roots; stems simple to 4–ca. 10, branching from near the base, these usually becoming buried, 3–6 (–10) cm long, sometimes also with stems above ground, these ascending 3–6(–21) cm long. Leaves thick sometimes leathery, green to gray-green, glabrous to densely strigillose or the hairs sometimes somewhat spreading, the hairs 0.2–0.6 mm long, usually more dense along the margins, obovate to linear-oblanceolate, (2.8–)7–16(–21) cm long, (0.3–)1–3(–5) cm wide, rounded to acute at the apex, coarsely and irregularly serrate or dentate sometimes pinnately lobed or subentire, the lobes usually cut less than halfway into the blade and often larger toward the base of the blade, the teeth mostly triangular, 0.5–5(–7) mm high, gradually tapering to a petiole (1–)3–7(–10) cm long. Buds erect. Flowers 1–4(–6) per stem opening per day. Ovary glabrous to sparsely strigillose, (7–)8–15(–20) mm long, sessile or on a short pedicel 1–2 mm long. Floral tubes (3.5–)4–6 (–8.5) cm long, 1–2 mm diam. medially, flaring 7–13 mm at the mouth, sparsely strigillose to glabrous, rarely (N Nevada and Oregon) sparsely glandular. Sepals green, the veins infused with a rich reddish purple pigment, (1.5–)2.4–3.5(–4) cm long, 2–5(–6) mm wide, glabrous or strigillose along the midvein. Petals fading rose pink to dark rose purple, (1.6–)2.5–4(–4.8) cm long, (2–)2.9–4.8(–5.5) cm wide, glabrous, the notch broad, 3–6 mm deep. Staminal filaments (12–) 15–24(–26) mm long; anthers 9–12 mm long. Style (4.5–)6–12 cm long; stigma lobes (3–)4–5 mm long. Capsules 3–6(–25) maturing per stem, lanceoloid to ovoid, obtusely quadrangular, falcate or sigmoid, becoming nearly straight at maturity, asymmetrical and often somewhat flattened, especially at the base, (1–)2–4(–5) cm long, 4–6 mm diam., tapering to a conspicuous sterile beak 4–8(–12) mm long, the free tips spreading to recurved, 1–2 mm long, the base cuneate to obtuse, glabrous to sparsely strigillose, the margins of the valves with a low to high and prominent sinuate-ridge with 5–10 peaks, or nearly distinct tubercles, these 0.5–2 mm high, 0.5–3 mm apart, the cross-veins inconspicuous or obscure, dehiscing ⅔–¾ their length, the valves spreading; sessile or on a short flattened pedicel (0.5–)1.5–3 mm long. Seeds 30–110 per capsule in two partially overlapping rows or rarely one irregular row in each locule, the raphe usually oblique to the plane of the capsular axis, narrowly obovoid, often curved, brown to dark reddish brown, 2.5–3.9 mm long, 1.2–1.7 mm wide, 1.1–1.3 mm high; embryo portion constituting about ½–⅔ of the seed volume, the surface papillose, the papillae conspicuous, often collapsed; seed-collar oblong, the membrane depressed deeply into the raphial cavity, the margin sinuate throughout or more typically sinuate only toward the distal end, the surface papillose, becoming reticulate toward the margins. Gametic chromosome number, $n = 7$.

Distribution (Fig. 103). Scattered or forming colonies in open sites on loose to hard, compacted clay or rarely more sandy soils, rocky slopes composed of shales, volcanics, or fine sandstones, gumbo flats, badlands, and bluffs or exposed rocky ridges, also often colonizing roadcuts, in grasslands, sagebrush or shadscale scrub or exposed sites in montane conifer forests from Yakima County, Washington and central Oregon to southern Alberta and Saskatchewan southeast to the Missouri River in South and North Dakota southwest to northern and east-central Colorado, along the Wasatch Range in Utah and the northwestern edge of Colorado Plateau Region, and from Emery County, Utah, west to White Pine

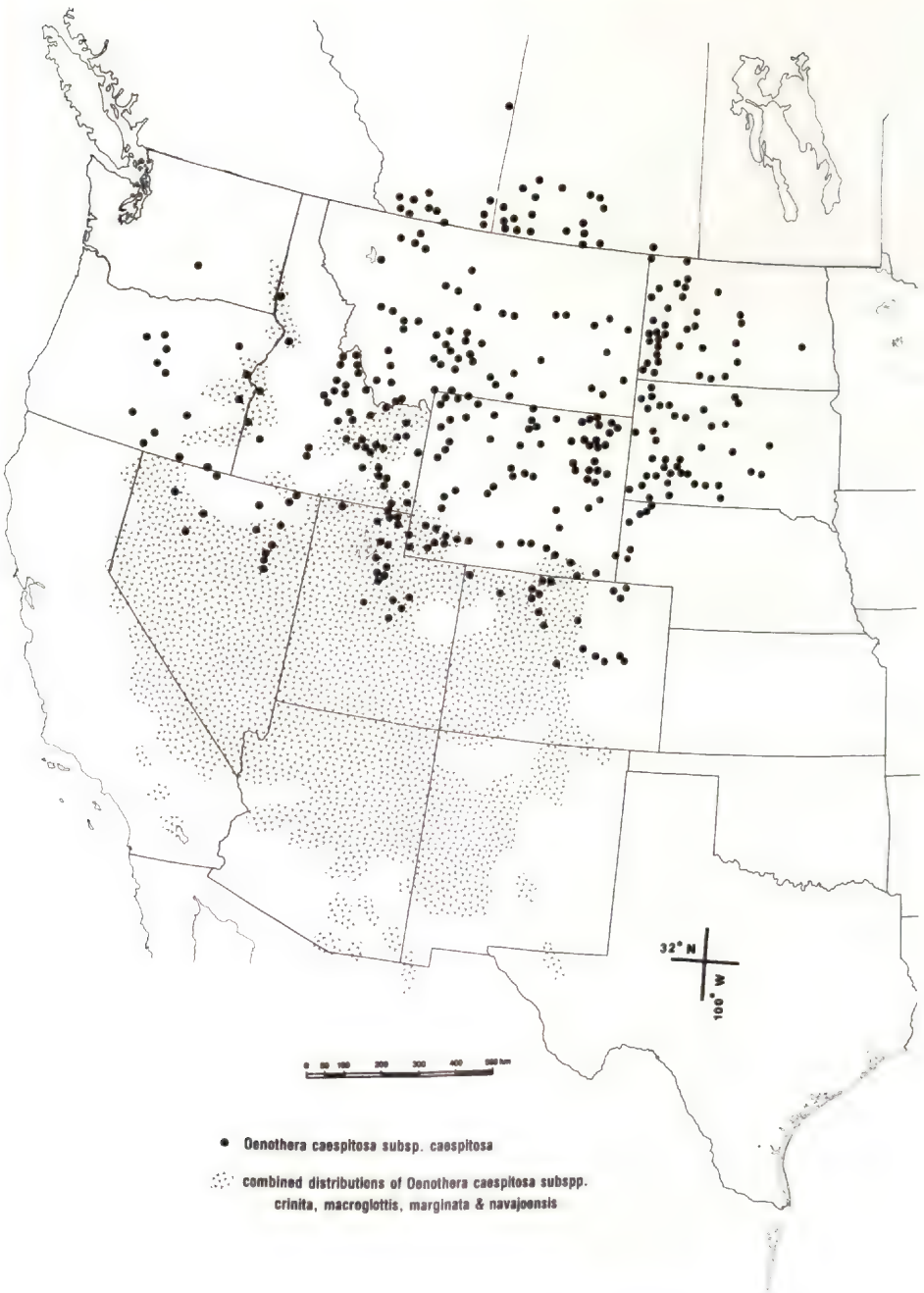

32° N
100° W
0 50 100 200 300 400 500 km
Oenothera caespitosa subsp. caespitosa
combined distributions of Oenothera caespitosa subspp.
crinita, macroglottis, marginata & navajoensis

FIGURE 103. Distribution of *Oenothera caespitosa* subsp. *caespitosa* relative to the combined distribution of the other four subspecies (shaded).

and Pershing Counties and northward in Nevada, 850–3,050 m. Flowering from mid-May through July.

Representative specimens examined. CANADA. ALBERTA: 5 mi. E of Standoff, *Bigelow 139* (UAC); Short Creek, *Millman 702* (DAO); Milk River at Allerston, *Boivin & Perron 12227* (ALTA, DAO, GH); Lost River Canyon, 7 mi. S of Manyberries Exp. Sta., *Boivin & Alex 9563* (ALTA, DAO, NY); 20 mi. N of Wildhorse on Hwy. 48, 1963, *Fabris s.n.* (UAC); Lethbridge, *Macoun 4949* (CAN, GH); Whiskey Gap, *Moss 915* (ALTA, DAO, GH); Irvine, 1926, *Terry s.n.* (DAO); Writing on Stone Prov. Park, *DeVries 2155* (DAO, UAC). SASKATCHEWAN: 12 mi. S of Cadillac, *Argus & Best 4823* (RM); Eastend, *Best & Gross 92* (SCS, UAC); 14 mi. NNW of Val Marie, *Bird 647* (DAO); 1 mi. SE of Estevan, *Boivin 13490* (DAO, NDA, NY); Twelve Mile Lake, 1938, *Bolton s.n.* (SCS); Swift Current, 1936, *Budd s.n.* (SCS); 10 mi. NW of Glen Kerr, *Coupland 169* (DAO); Moose Jaw, *Cowles 58* (F, MO); Big Muddy Valley, *DeVries 954* (DAO); Drinkwater, *Hood 6* (CAN, DAO, RM); Frenchman Creek, *Looman 12598* (SCS); 15 mi. S of Bengough, *Love & Boivin 6375* (WIN); Cypress Hills, *Macoun 10620* (ALTA, CAN); 2 mi. E of Avonlea, *Ledingham & Rawlingson 49-125* (DAO); Matador, *Witidsdale 42-38* (SCS); Consul, *Tidsdale 42-68* (SCS). UNITED STATES. COLORADO: Boulder Co., 1.3 mi. N of Broomfield, *Wagner 4017* (MO). Douglas Co., 15 mi. W of Castle Rock, *Beetle 2376* (CAS, NY). Elbert Co., 3 mi. NW of Fondis, *Owenby 1279* (COLO, GH, MO, MONT, NY, RM, UC, UTC, WS). El Paso Co., near Rama, *Moldenke 19411* (PH, RSA). Grand Co., 4 mi. N of Kremmling, *Osterhout 3478* (RM). Jackson Co., 4.1 mi. NE of jct. Hwy. 40 & 14, *Wagner 4038* (MO). Lincoln Co., 9 mi. SE of Limon, U.S. Hwy. 40, *Raven & Gregory 19497* (DS, RSA). Logan Co., 38 mi. NW of Sterling, *Stephens 55911* (KANU). Moffat Co., Lodore Canyon, *Harrington 1527* (CS). Park Co., South Park, 1871, *Canby s.n.* (NY). Routt Co., 1.1 mi. N jct. Hwy. on road to Clark, *Wagner 4044* (MO). Summit Co., 12 mi. N of Rock Creek turnoff, *McCreary 86* (CS). Weld Co., 16.5 mi. N of Raymer, *Stephens 55961* (KANU, NY). IDAHO: Bannock Co., Pocatello, Red Hill, 1940, *Olson & Bergstrom s.n.* (BH, DS, ID, UC). Bear Lake Co., Montpelier, *Macbride 19* (E, G, GH, MIN, MO, RM). Blaine Co., Martin, *Macbride & Payson 3042* (E, GH, MO, NY, RM, US). Bonneville Co., 10 mi. SW of Swan Valley, *Christ & Christ 18912* (NY). Butte Co., 5 mi. W of Martin, Iron Mt., *Hitchcock et al. 3824* (CAS, US). Bingham Co., 2 mi. N of Midway, *Cronquist 2338* (GH, IDS, MO, UTC). Caribou Co., near Soda Springs, 1892, *Mulford s.n.* (GH, MIN, MO, NY). Clark Co., 5 mi. from head of Medicine Lodge Creek, *Davis 3137* (IDS). Custer Co., Challis, *Macbride & Payson 3230* (CAS, DS, E, GH, MO, NY, POM, RM, UC, US). Franklin Co., 22 mi. SE of Preston, *Christ & Christ 19870* (ID). Fremont Co., 25 mi. NW of St. Anthony, 1959, *Chadwick s.n.* (ID). Gooding Co., confluence of Clover Creek and E Fork of Clover Creek, *Ertter 75-117* (ID). Idaho Co., 10 mi. S of White Bird, Salmon River Canyon, *Hitchcock & Muhlick 8490* (DS, GH, NA, NY, RM, UC, UTC, WS). Jefferson Co., 6 mi. N of Menan, *Christ 53-82* (ID). Lehmi Co., 10 mi. S of Gibbonsville, *Hitchcock et al. 3698* (CAS, DS, LA, NA, RM, UC, UTC, WS). Madison Co., W of Rexburg, *Cronquist & Davis 2074* (MO). Nez Perce Co., rocky slopes at Lewiston, *Sanborg et al. 185* (MIN). Owyhee Co., 5 mi. E of Murphy, *Maguire & Holmgren 26200* (GH, NY, RSA, UC, US, UTC). Power Co., 15 mi. NW of American Falls, Snake River Plain, *Holmgren & Holmgren 4802* (ASU, BRY, NY, US, WTS). Washington Co., 10 mi. below Weiser, 1946, *Davis s.n.* (IDS). MONTANA: Beaverhead Co., 18 mi. S of Dillon, *Barkley & Reed 4002* (MONT, ND, US). Broadwater Co., 7 mi. E of Townsend on Hwy. 12, *Stockhouse 131* (MO). Carbon Co., 40 mi. S of Billings, Bull Mts., 1882, *Canby s.n.* (NY). Carter Co., near Ekulaka, *Louisik 2* (MONT, ND, US). Cascade Co., Great Falls, *Williams 12* (MIN, US). Chouteau Co., 6 mi. N of Loma, *Stephens 68583* (KANU). Custer Co., 2 mi. E of Locate, *Stephens 67036* (KANU). Dawson Co., 9 mi. NW of Lindsay, *Stephens 67402* (KANU). Fergus Co., 20 mi. S of Lewiston, Big Snowy Mts., *Hitchcock & Muhlick 11907* (NY, WS). Gallatin Co., Sedan, 1901, *Jones s.n.* (GH, MICH, MONT, RM). Garfield Co., 19.5 mi. W of Jordan, 1952, *Anderson & Scharff s.n.* (KANU). Glacier Co., Cutbank, *Moss 3299* (ALTA). Granite Co., 40 mi. E of Missoula, *Hitchcock 2992* (CAS, CS, DS, MO, MONT, POM, RM, WS). Judith Basin Co., 5 mi. E of Stanford, *Hitchcock 16113* (CAN, DS, NY, RSA, UC, UTC, WS). Lake Co., Swan Lake Valley, 1888, *Knowlton s.n.* (CAN). Lewis & Clark Co., Haystack Butte, *Lackschewitz 4264* (MONTU). Meagher Co., E border of county on Rt. 6, 28 mi. from Harlowton, *Booth 55372* (GH, RM). Park Co., Livingston, *Blankinship 696* (CAN, F, US). Pondera Co., Dupuyer Creek, 5.8 mi. W of Valier, *Bartlett & Grayson 414* (DS, MIN, NY). Powder River Co., 10 mi. S of Broadus, *Stephens & Brooks 23820* (DS, KANU). Powell Co., Deer Lodge, 1888, *Traphagom s.n.* (MICH, NY). Prairie Co., Watkins, *Naasz 1075* (MONT). Rosebud Co., Ft. Union Basin, *Lackschewitz 5952* (MONTU). Sheridan Co., Westby, *Larsen 37* (GH, MO). Stillwater Co., Jacksonte Creek, Absarokee, 1923, *Hawkins s.n.* (WIS). Sweetgrass Co., Crazy Mts., *Hitchcock & Muhlick 13315* (NY). Wheatland Co., 15 mi. SW of Harlowton near Big Elk Creek, *Hitchcock 2417* (MONT, POM). Yellowstone Co., 14 mi. N of Billings along Rt. 3, *Davidse & Collotzi 665* (UTC). NEBRASKA: Dawes Co., 14 mi. E Crawford, *Stephens & Brooks 24712* (DS). Scotts Bluff Co., Scotts Bluff Nat'l. Monument, *Stephens 5391* (GH, KANU, UMO). Sioux Co., without locality, *Kramer 89* (MO). NEVADA: Elko Co., Elko, *Kennedy 4293* (DS, PH, UC); East Humboldt Mts., E of Angel Lake, *Raven & Solbrig 13484* (NY, RSA, UC). Humboldt Co., Buckskin Mt., Santa Rosa Range, *Tiehm & Williams 1299* (NY, RENO). Pershing Co., N of Star Creek, E side of Star Peak, *Ownbey & Ownbey 2859* (WS). White Pine Co., S side of Sherman Ridge, S end of Ruby Range, *Hitchcock & Martin 5628* (DS, GH, NA, NY, POM, UC, UTC). NORTH DAKOTA: Barnes Co., Valley City, *Haigh 388* (SDU). Billings Co., 25 mi. N of Belfield, *Zaczkowski 2704* (NDA). Burke Co., Short Creek Dam, 7 mi. N of Colombus, *Hegstad 7893* (NDA). Bowman Co., Bowman, 1918, *Stevens s.n.* (NDA). Burleigh Co., Twin Buttes, *Keammerer 93* (NDA). Divide Co., 1 mi. E of Westby, *Hegstad 8946* (NDA). Dunn Co., 6 mi. S and 3 mi. W of Halliday, *Rohde 14* (NDA). Emmons Co., 3 mi. S of Glencoe

Church, *Williams 114* (KANU, NDA). Golden Valley Co., 4 mi. E and 20 mi. N of Sentinel Butte, *Zaczkowski 3609* (NDA). Grant Co., Pretty Rock, *Bell 1169* (NDA). McKenzie Co., 13 mi. S Watford City, *Stephens & Brooks 40240* (KANU). McLean Co., 10.5 mi. S Raub, *Stephens & Brooks 12828* (KANU). Morton Co., Glen Ullin, 1935, *Stevens & Kleunder s.n.* (BRY, CAN, DAO, F, MIN, UC, WIS). Mountrail Co., 7 mi. S and 3 mi. W of Powers Lake, *Hegstad 3092* (NDA). Sheridan Co., 20 mi. N McClusky, *Stevens 2087* (DAO, MIN, UC, US). Sioux Co., Hwy. 6, N of Shields Rd., *Stevens in 1970* (NDA). Slope Co., Marmarth, *Moyer 430* (MIN). Stark Co., Dickinson, 1908, *Holgate s.n.* (GH, NY). Ward Co., Minot, *Lakela 455* (MIN). Williams Co., 1 mi. E of Williston, *Hegstad 7766* (NDA). OREGON: Baker Co., Hwy. 30 between Huntington and Lime, *Wann 4669* (UTC). Crook Co., near Crooked River, *Cusick 2633* (CU, E, F, G, GH, MIN, MO, NY, POM, RM, UC, US, WS). Harney Co., 2 mi. SW of Narrows, *Peck 13970* (DS, F, WILLU). Jefferson Co., 15 mi. NE of Madras, *Peck 13798* (DS, PH, POM, WILLU). Lake Co., S end of Summer Lake, *Peck 15681* (WILLU). Malheur Co., 6 mi. NW of McDermitt, *Peck 25682* (WILLU), *Peck 25712* (CAS, UC, WILLU). Union Co., hills of Powder River, *Cusick 842* (WS). Wheeler Co., above Clarno, John Day Valley, *Wagner 4466* (MO). SOUTH DAKOTA: Brule Co., Chamberlain, *Lee 513* (RM). Butte Co., near Hay Creek, 1975, *Sisk s.n.* (SDU). Carson Co., Wakpala, *Moyer 2595* (MIN). Custer Co., 2 mi. S of Fairburn, *McIntosh 1371* (NY). Dewey Co., 11.5 mi. SE of Eagle Butte, *Stephens 12260* (DS, KANU). Fall River Co., 10 mi. W of Edgemont, *Craig 3465* (POM). Haakon Co., 9 mi. N and 11 mi. E of Billsburg, *Stephens 12189* (DS, KANU). Hand Co., Slim Buttes, *Moore 2068* (MIN). Harding Co., Cave Hills, *Over & Salem 9694* (SDU). Jackson Co., between Norbeck Pass and Cedar Pass, *Lindstrom 62* (SDU). Lyman Co., above Missouri River opposite Chamberlain, *Palmer 36093* (GH, MO). Meade Co., S of Bear Butte Creek, *Benson 616* (NA). Mellette Co., 5 mi. N of Norris, *Stephens & Brooks 39160* (KANU). Pennington Co., W of Cedar Pass, *Craig 3447* (POM). Perkins Co., SE corner of Perkins County, *Eminger 530* (NA). Shannon Co., 25 mi. NW of Sharps Corner, *Stephens & Brooks 39338* (KANU). Stanley Co., Ft. Pierre, *Beall 12* (NA). Todd Co., Badlands, *Beuchal 14896* (US). Walworth Co., Mobridge, *Moyer 397* (CU, NY). Washabaugh Co., 7 mi. E and 2 mi. N of Wanblee, *McGregor & Bare 1230* (KANU). UTAH: Box Elder Co., Wellsville Mts., Two Jump Canyon, 0.5 mi. W of Relay Station, *Wagner 4066* (MO). Cache Co., Logan Canyon, *Maguire 3606* (CU, MO, RM, UC, UTC). Carbon Co., Price Canyon, W of Summit, *Malbutt 37* (UT). Emery Co., Seeley Creek, 1936, *Crane s.n.* (NY). Juab Co., small creek (T31S, R2E, Sec. 8), *Collins & Harper 134* (BRY). Morgan Co., Huntsville-Mountain Green Rd., N of Hwy. 30, *Perdue 6213* (NA). Salt Lake Co., Parleys Canyon, *Garrett 1550* (NY). Summit Co., Kimball Jct., 1908, *Clemens s.n.* (DS). Utah Co., American Fork Canyon, *Gooding 1172* (GH, MO, NY, RM). Wasatch Co., near Midway, *Carlton & Garrett 6681* (CAN, GH, NY, RM). Weber Co., Weber Canyon, *Flowers 450* (UT). WASHINGTON: Yakima Co., Priest's Rapids, Columbia River, *Tweedy 787* (DS, GH, NY, PH, YU). WYOMING: Albany Co., Laramie, Red Hills, *Nelson 1221* (E, F, MIN, NY, POM, RM, UT, WIS, WS), *Nelson 6952* (COLO, GH, KANU, MIN, MO, NDS, NESH, NY, POM, RM, UT), *Wagner 4033* (MO). Big Horn Co., 20 mi. E of Greybull, Shell Canyon, *Walker 2400* (PH). Campbell Co., 8.5 mi. N of Soda Well, *Dueholm & Hartman 1402* (KANU, MO, RM). Carbon Co., 4 mi. N of Medicine Bow, *Stephens 70466* (KANU). Converse Co., 1 mi. S of Antelope Creek on County Rd. 37, *Hartman & Dueholm 5852* (KANU, MO, RM). Crook Co., Hulett, *Ownbey 609* (COLO, GH, MO, MONT, NY, RM, UC, UTC, WS). Fremont Co., 15 mi. W of Dubois on Hwy. 287, *Stockhouse 134* (MO). Goshen Co., 4 mi. W of Lagrange, *Dorn 2022* (CAN). Johnson Co., 4 mi. N of I-90 at Power River Crossing, *Hartman & Sanguinetti 7427* (MO, RM). Laramie Co., 7.2 mi. W of Cheyenne, outcrop ⅓ mi. S of I-80, *Wagner 4024* (MO). Lincoln Co., 7.2 mi. E of jct. Hwy. 89 and 30 N on 30 N, *Stockhouse 128* (MO); Hwy. 30, 3.3 mi. E of Hwy. 189 jct., *Wagner 4045-A, 4045-C* (MO); 5.3 mi. E of Hwy. 189-30 jct. on Hwy. 30, *Wagner 4057-B* (MO). Natrona Co., Bates Hole, *Payson & Payson 4776* (RM). Niobrara Co., 5 mi. N of Manville, *Stephens 65899, 77492* (KANU). Park Co., Yellowstone Park, Golden Gate, *Nelson & Nelson 5530* (BM, CU, DS, E, G, GH, MIN, MO, NDS, NMC, NY, POM, RM, US). Sheridan Co., Sheep Mts., hills of Sheridan, *Sharp 343* (RM). Sublette Co., Big Piney, *Payson & Payson 4358* (GH, MO, PH, RM, WS). Sweetwater Co., S of Green River, Gumbo Flats, *Williams 403* (CAS, GH, MO, NY, RM, UC, UTC). Teton Co., below Gros Ventre Slide, Teton Nat'l. Forest, *Gregory 457* (CAS, DS, GH, RSA, SD, UC, UT); 1.1 mi. W of Grand Teton Nat'l. Park on Hwy. 287, *Stockhouse 133* (MO). Uinta Co., near Lyman, *Rollins 1635* (G, MO, ND, NY, RM, WS). Washakie Co., Big Horn Mts., Tensleep Creek, *Stolze 577* (F, WIS). Weston Co., 4 mi. SSE of Rochelle, *Hartman et al. 6760* (BRY, MO, RM).

Intermediates between *Oenothera caespitosa* subsp. *caespitosa* and subsp. *crinita*:

NEVADA: Elko Co., E of Wells, *Eastwood & Howell 313*, pro parte (subsp. *crinita* also present, CAS); 55 mi. S of Elko, *Holmgren 828* (UTC); 2 mi. SE of Elko, *Martineau 73*, pro parte (subsp. *crinita* present, NESH, RENO, UTC), *Tiehm 6106* (MO), *Wagner 4473* (MO). Humboldt Co., 36 mi. W of Battle Mountain, *Maguire & Maguire 5795* (CU, GH, UTC); 12.3 mi. W of Valmy, roadside (one plant), *Wagner 4472* (MO). Lander Co., Fish Creek Mts., *Tiehm 6047* (MO). Pershing Co., E side Tobin Range, S of Dacies Pass, *Tiehm & Birdsey 5659* (MO).

Intermediates between *Oenothera caespitosa* subsp. *caespitosa* and subsp. *marginata*:

IDAHO: Bannock Co., 8 mi. SW of Portneuf, S fork of Mink Creek, *Christ & Christ 19920* (ID, WS); Pocatello, Chinks Peak, 1942, *Evans s.n.* (ARIZ). Bingham Co., East Butte (T1N, R30E), *Atwood 1007* (BRY, NY). Blaine Co., Martin (mixed with subsp. *caespitosa*), *Macbride & Payson 3042* (E). Caribou Co., Wood Canyon, *Grimes 76-160* (ID). NEVADA: Elko Co., 24 mi. S Nevada-Idaho line on Hwy. 93 (road cut), *Klein 1156* (RSA, UC). Humboldt Co., Jackson Mts., Jackson Creek, *Holmgren & Holmgren 4054* (BARY, NY). UTAH: Cache Co., Pine Canyon, *Maguire 3044* (UTC). Duchesne Co., Indian Canyon (road cut), *Garrett 7787* (F, UT). Salt Lake Co., Parley's Canyon, *Cottam 7636* (UT), *Garrett 2140* (UT), *Wagner 4067* (MO). Sevier

Co., 20 mi. W of Richfield, Solitude Guard Station, *Coles 66* (BRY). Utah Co., Mt. Timpanogos, Wasatch Mts., *Gourley 8062a* (UC); 1.5 mi. NE of Provo, *Harston 6178* (BRY); Pole Canyon (road cut), *Nixon 76* (BRY); Squaw Peak Loop, Provo Canyon, *Patrick 121* (BRY). Weber Co., Ogden, 1871, *Hayden s.n.* (mixed with subsp. *caespitosa*, PH). WYOMING: Lincoln Co., 3.3 mi. E of jct. Hwy. 180 on 30 N (road cut), *Wagner 4054C* (mixed with subsp. *caespitosa* and subsp. *marginata*, MO).

Oenothera caespitosa subsp. *caespitosa* resembles the common form of subsp. *crinita* in its acaulescent or very short-stemmed habit, flowers that fade to a rose purple color, falcate or sigmoid capsules that are asymmetrical at the base, and seed-collars with internal ribbing, but subsp. *caespitosa* is unique in its strigillose pubescence (sometimes glabrous) and the complete lack of glandular hairs. General variations in the density of the strigillose pubescence in *O. caespitosa* subsp. *caespitosa* have been recognized formally: (1) Densely pubescent plants from Nevada, Idaho, and Washington have been referred to *O. caespitosa* var. *purpurea* [Munz (1931b) or as a subspecies by Munz (1965)]; (2) the densely pubescent plants from Washington as *Pachylophus canescens*; and (3) glabrous plants from eastern Wyoming as *Pachylophus glaber*. Although there is a tendency for plants from a particular geographical area to be similar in density of pubescence, there is far too much parallel development in density in many areas and overall the variation is too continuous to warrant formal recognition.

One series of populations from southeastern Wyoming and adjacent Weld and Logan Counties, Colorado is atypical in that the plants have hairs 0.5–1 mm long rather than 0.2–0.6 mm long. Moreover, the hairs are spreading rather than appressed and also somewhat crinkly. Features of the leaves, flowers, and fruits seem specialized in that each is at the small end of the range for this subspecies. Based on the hair characters, the most likely hypothesis for the origin of this long-haired form of *Oenothera caespitosa* subsp. *caespitosa* is that it may have originated following hybridization with *O. caespitosa* subsp. *macroglottis*. These populations are intermediate geographically and ecologically, occurring in more coarsely textured soil than most populations of subsp. *caespitosa*.

Two populations of the form with long hairs were studied in southeastern Wyoming. One was located on red sandy soils near Laramie, Albany County, Wyoming (*Wagner 4033*). Textural analysis of the substrate of this site was a gravelly sandy loam composed of 56% sand, 33% silt, and 11% clay. The clay fraction in this sample is considerably lower than usual for *Oenothera caespitosa* subsp. *caespitosa* which has a known range of 35–55% clay based on four samples selected for analysis from across its range. In fact, the texture of the soil at the Laramie site is more similar to that seen in 20 samples of soil from localities where *O. caespitosa* subsp. *macroglottis* grew. These were analyzed by Goeken (1968), and had mean values 79% sand, 12% silt, and 11% clay. The second population was 11.5 km west of Cheyenne, Laramie County, Wyoming (*Wagner 4024*). This site was a crumbly conglomerate outcrop in a grassland. The texture of the soils here was not tested, but the coarse gravelly soils were clearly atypical for subsp. *caespitosa*. The exact distribution of this entity should be studied in relation to other populations of the subspecies in the region.

Nuttall described *Oenothera montana* from a collection of the long-haired form, but the name was soon applied to many other elements of *O. caespitosa* in which the pubescence was confined to the margins of the leaves. When Munz (1931b) published his revision, he adopted the epithet *montana* for his broadly circumscribed *O. caespitosa* var. *montana*, without having seen the type material of Nuttall's taxon. Since at least some plants of all subspecies have their pubescence confined to the margins of the leaves, the resulting entity was highly artificial.

1c. Oenothera caespitosa Nutt. subsp. **navajoensis** W. L. Wagner, Stockhouse & Klein, subsp. nov. TYPE: Along Paria River, 8 mi. NW of Hwy. 89A (T42S, R1W, Sec. 4), Kane Co., Utah, 1,370 m, 28 May 1965, *Cronquist 10202* (holotype, UTC-120458, photo MO; isotypes, BRY, DAO, DS, NY, RSA). Figure 104.

Pachylophus caulescens Rydb., Bull. Torrey Bot. Club 31: 571. 1904. TYPE: Palisades, Mesa Co., Colorado, 1,450 m, 14 May 1898, *Crandall 12* (holotype, NY, photo MO). Rydb., Fl. Rocky Mts. 598. 1922.

Oenothera caespitosa var. *jonesii* sensu Munz, Amer. J. Bot. 18: 731. 1931, pro parte (as to all but the type), non Munz. Harrington, Man. Pl. Colo. 396. 1954. Kearney & Peebles, Ariz. Fl. Ed. 2, 598. 1960; McDougall, Seed Pl. N. Ariz. 334. 1973. Lehr, Cat. Fl. Ariz. 109. 1978. *Oenothera caespitosa* subsp. *jonesii* sensu Munz, N. Amer. Fl., Ser. II, 5: 101. 1965, pro parte.

FIGURE 104. *Oenothera caespitosa* subsp. *navajoensis*; Grand Co., Utah, *unknown collector #20* (NY).

Oenothera caespitosa var. *montana* sensu Munz, Amer. J. Bot. 18: 732. 1931, pro parte, non (Nutt.) Durand, Kearney & Peebles, Ariz. Fl. Ed. 2, 598. 1960, pro parte; McDougall, Seed Pl. N. Ariz. 334. 1973, pro parte; Lehr, Cat. Fl. Ariz. 109. 1978, pro parte. *Oenothera caespitosa* subsp. *montana* sensu Munz, N. Amer. Fl., Ser. II, 5: 101. 1965, pro parte.

Herba perennis caulescens vel raro acaulescens, radicis secundariis plus elongatis surculos novos edentibus. Caules prope basin plerumque 6–12 ramosi raro simplices, 1–2.5 dm longi. Folia crassa, moderate vel dense villosa pilis minutis glandulosis praedita, oblanceolata vel rhomboideo-ovata, grosse et irregulariter dentata, raro pinnate lobata. Tubus floralis (3.5–)4.2–6.4(–7) cm longus. Petala alba demum subrosea, (2.5–)2.8–3.2(–3.4) cm longa, (2.9–)3.2–4(–4.4) cm lata. Capsula oblongo-lanceoloidea, conspicue quadrangularis, recta, 1.3–3.5(–4) cm longa, valvularum marginibus porca sinuata humili vel tuberculis 8–15 fere distinctis, 0.4–1 mm altis praeditis, per dimidium vel duos longitudinis trientes dehiscens, tum valvis rectis vel incurvatis. Numeri chromosomatici gametici, $n = 7, 14$.

Caulescent and loosely caespitose to acaulescent perennial herb from a taproot with slender spreading lateral roots which produce adventitious shoots; stems, if present, from a leafy rosette, 1–2.5 dm long, simple with 6–12 lateral branches arising from near the base, these sometimes with a few secondary branches, straw-colored to reddish purple. Leaves grayish green to green, thick, moderately to densely crinkly villous, the hairs usually somewhat tangled, erect or spreading, 0.5–1.2 mm long, mixed with minute glandular hairs, 0.1–0.2 mm long, the hairs usually more dense on the upper surface of the leaves, often giving a shaggy appearance, sometimes restricted along the margin and major veins, oblanceolate to rhombic-obovate, (3.5–)4–13 (–16) cm long, (0.7–)1–3.2 cm wide, acute to rounded at the apex, coarsely and irregularly dentate or serrate, sometimes pinnately lobed, often with several larger lobes toward the base of the blade, the teeth narrowly to broadly triangular, mostly 1–3 mm high, the larger lobes 4–7 mm high, abruptly tapering to a long petiole

(1.3–)1.7–10(–12) cm long. Buds often recurved during early development. Flowers 1–3(–6) per stem opening per day. Ovary densely villous and glandular, sometimes only glandular, 8–21 mm long, on a short pedicel 1–3 mm long. Floral tubes (3.5–)4–7(–8) cm long, 1–1.5(–2) mm diam. medially, flaring to 7–10 mm at the mouth, sparsely to densely villous and glandular pubescent to mostly glandular pubescent. Sepals green to yellowish green, the veins often infused with reddish purple pigment, 2.2–2.7(–3.2) cm long, pubescence the same as the floral tube, usually more densely hairy along the midvein. Petals fading pink to light rose, (2.5–)2.8–3.2(–3.4) cm long, (2.9–)3.2–4(–4.4) cm wide, the notch 7–9 mm deep, glabrous. Staminal filaments 11–15 (–17) mm long; anthers 9–12 mm long. Style (5–)5.9–8.5(–9.6) cm long; stigma lobes (3–)4–7 mm long. Capsules 4–25(–32) maturing per stem, oblong-lanceoloid, quadrangular or sometimes only obscurely angled in cross-section, straight, asymmetrical at the base, which is also usually truncate to rarely obtuse, 1.3–3.5(–4) cm long, 5–6 mm diam., abruptly tapering to a conspicuous sterile beak 6–17 mm long, the erect free tips ca. 2 mm long, moderately villous and glandular pubescent becoming glabrate, the margins of the valves with a low sinuate ridge to 8–15 small nearly distinct tubercles, 0.4–1 mm high, 2–3 mm apart, the cross-veins prominent, dehiscing ½–¾ their length, the valves remaining erect or incurved; pedicel flattened to rounded, 1–3 mm long. Seeds 50–115 per capsule in two adjacent and distinct rows, the raphe parallel to the plane of the capsular axis, narrowly obovoid, often somewhat curved, light to dark reddish brown to nearly black, 2.1–2.6 mm long, 1.1–1.3 mm wide, 1.1–1.5 mm high; embryo portion constituting less than ½ of the seed volume, the surface papillose with large papillae, sometimes appearing smooth (reticulate under high magnification); seed-collar completely sealed by a broad often undulate membrane, the seed-collar margin entire or sometimes the distal end inconspicuously sinuate, the surface finely reticulate, often appearing striate under low magnification. Gametic chromosome numbers, $n = 7$, 14.

Distribution (Fig. 105). Forming small colonies on loose or compacted soil derived from clays, shale, fine-textured sandstone, or gypsum, occurring on slopes and along small drainage patterns, often around harvester ant mounds, occasionally along arroyos in somewhat sandy or gravelly soils, generally in shrubby communities dominated by *Atriplex corrugata* S. Wats., *A. cuneata* A. Nels., *A. confertifolia* S. Wats., *Artemisia spinescens* Eaton, *Frankenia jamesii* Torrey, *Coleogyne ramosissima* Torrey, and *Hilaria jamesii* (Torrey) Benth., but sometimes with bigsage scrub or sage-grasslands, rarely in lower pinyon-juniper woodland, endemic to the Colorado Plateau Region, from Daggett County, Utah southwest to eastern Washington County, Utah, eastward across northern Arizona to San Juan County, New Mexico, with disjunct populations in Central Sandoval County, New Mexico, 1,100–1,850(–2,100) m. Flowering from mid-April through mid-June, rarely later. A collection from 3 mi. W of Holbrook, *Degener 4057* (NY), Navajo County, Arizona, if actually collected from this area, is a surprising disjunct of some 100 km south of any other known locality in Arizona. This locality needs to be confirmed.

Representative specimens examined. UNITED STATES. ARIZONA: Apache Co., 8 mi. NE of Rock Point, *Peebles & Smith 13534* (ARIZ, CAS, US). Coconino Co., 15 mi. N of Cameron, *Ripley & Barneby 8498* (CAS, NY, RSA). Navajo Co., N of Kayenta, Capitan, *Peebles & Fulton 11914* (ARIZ, US). COLORADO: Dolores Co., Lone Cone, *Brewster s.n.* (COLO). Delta Co., NW of Eckert, George Creek, *Weber 7532* (COLO, WS). Garfield Co., 7 mi. SW of Grand Valley, *Harrington 4292* (CS). Mesa Co., opposite Highline Lake, 5.8 mi. N of jct. Hwy. 139 & 6, *Wagner 4511* (MO). Montezuma Co., S of Cortez, *Clark 14473* (UNM). Montrose Co., Cedar Creek, *Payson 1040* (MO, RM). Rio Blanco Co., 2 mi. SE of mouth of Wolf Creek, on White River, *Graham 9075* (POM, US). NEW MEXICO: Sandoval Co., 3.5 mi. SW of San Ysidro, *Wagner et al. 4405* (MO). San Juan Co., ¾ mi. N of Rt. 550 on county rd. 52, *Marley 1808* (MO, NMC, NY, UNM). UTAH: Carbon Co., Price, *Mosquin & Mulligan 5024* (DOA, DS). Daggett Co., vicinity of Flaming Gorge, *Williams 455* (MO, NY, RM, UC). Duchesne Co., 35 km SE of Myton, *Cronquist 11389* (BRY, NY, UMO, UTC). Emery Co., Sinbad, 13 mi. from Green River, *Welsh & Taylor 14651* (BRY, NY, WTS). Garfield Co., Eggnog Spring, Bullfrog Creek, W of Henry Mts., *Welsh 3964* (BRY, NY). Grand Co., W slope of LaSal Mts., *Rydberg & Garrett 9084* (CAN, NESH, NY, RM, US, UT); Colorado River Canyon, 1 mi. E of Salt Wash, *Stockhouse 216* (MO); Colorado River Canyon, 2 mi. W of Salt Wash, *Stockhouse 532* (MO); Colorado River, 1 mi. E of turnoff toward Salt Wash, *Stockhouse 534* (MO); 2 mi. E of Moab along Colorado River, *Wagner 4509* (MO); 4.2 mi. S of jct. Hwy. 128 and rd. to Cisco, *Wagner 4510* (MO); 16 mi. S of Green River, *unknown collector 20* (NY). Kane Co., 10.2 mi. E of Zion Nat'l. Park, Hwy. 15, *Morris et al. 160* (MO); San Juan Co., jct. of Nokai Creek & San Juan River, *Cutler 2271* (CAS, GH, MNA, MO, UC, WIS); Blue Notch, *Stockhouse 547* (MO); Lake Powell, *Stock-*

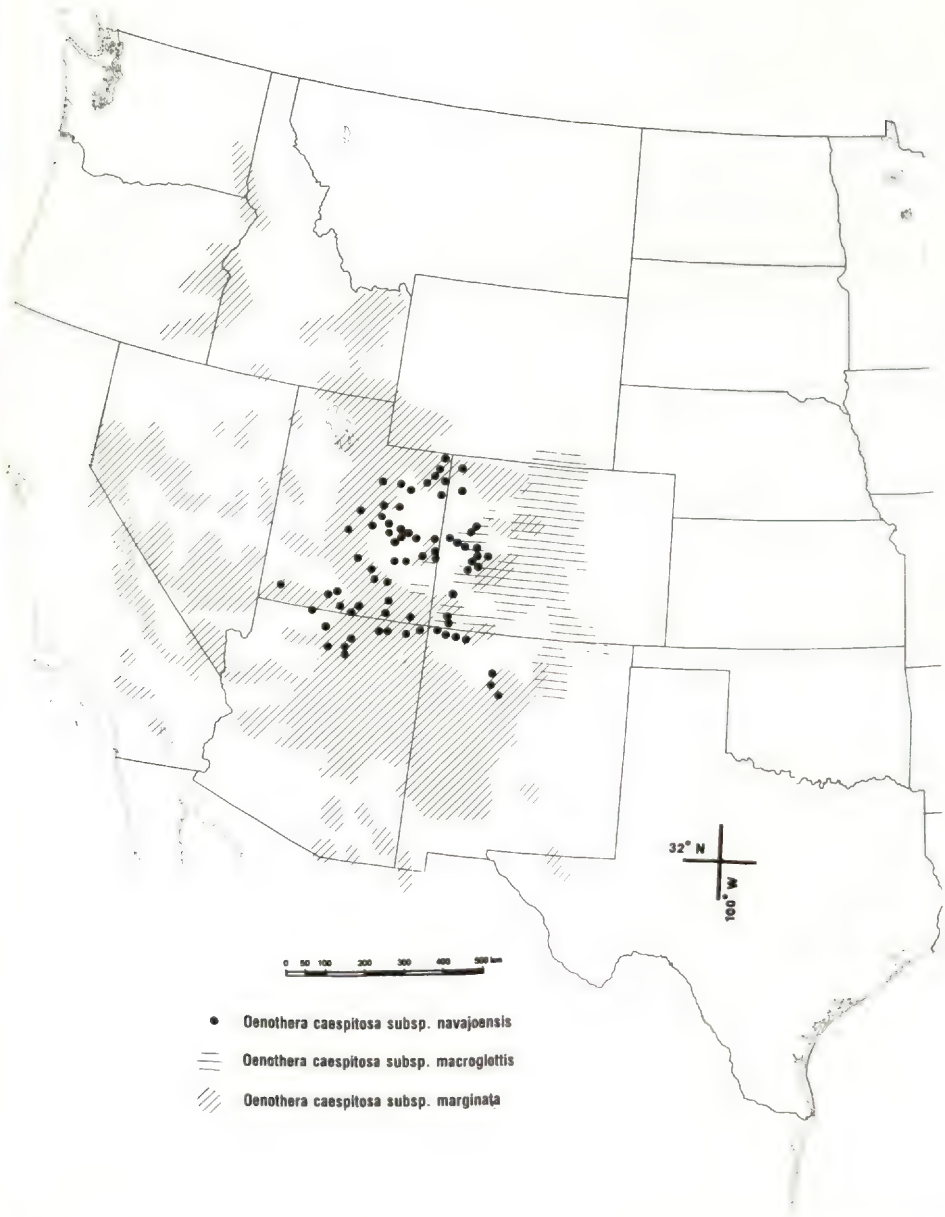

32° N
100° W
0 50 100 200 300 400 500 km
Oenothera caespitosa subsp. navajoensis
Oenothera caespitosa subsp. macroglottis
Oenothera caespitosa subsp. marginata

FIGURE 105. Distribution of *Oenothera caespitosa* subsp. *navajoensis* relative to the distributions of *O. caespitosa* subspp. *macroglottis* and *marginata* (shaded).

house 548, 549 (MO). Sanpete Co., Moroni, *Eastwood & Howell 596* (CAS). Sevier Co., 15 mi. SE of Sigurd, *Maguire 18093* (BRY, NY, UTC). Uintah Co., 1 mi. S of jct. of Ouray Rd. and U.S. 40, *Welsh 36* (BRY, MO, SDU, UT). Wasatch Co., Strawberry River below Stinking Springs, *Howard 103* (NA). Washington Co., S of Pine Valley, *Plummer 7397* (RSA). Wayne Co., 5 mi. NE of Hanksville, *McVaugh 14580* (CAS, MICH, NY).

Intermediates between *Oenothera caespitosa* subsp. *navajoensis* and subsp. *marginata*:

ARIZONA: Coconino Co., near Tuba City, *Peebles & Fulton 11854* (ARIZ, US). COLORADO: Mesa Co., Palisade, *Crandall 12* (RM). Moffat Co., Mouth of Hell

Canyon and jct. of Yampa Canyon, *Harrington 3925* (ARIZ). UTAH: Grand Co., along Colorado River, 1 mi. E of Moab Bridge (mixed with subsp. *navajoensis*), *Bryan & Moab School 1-16* (UTC); 15 mi. NW of Moab (mixed with subsp. *navajoensis*), *Harrison 5961* (BRY); Arches Nat'l. Monument, Balanced Rock (mixed with subsp. *navajoensis, Harrison 11262A*), *Harrison 11262* (BRY, US); 5 mi. S of Moab (mixed with subsp. *navajoensis*), *Harrison et al. 10301* (BRY); 15 mi. E of Green River, 1968, *Kleiner & Harper s.n.* (UT); 5 mi. N of Thompson, *Northstrom 86* (BRY). Kane Co., Kaiparowits Plateau (T40S, R7E, Sec. 34), *Atwood & Trotter 5269* (BRY, RM, WTS); 10.2 mi. E of Zion Nat'l. Park on Hwy. 15 (1 plant), *Morris et al. 160* (MO); Lake Powell, Dry Rock Creek, *Welsh & Atwood 11619* (BRY). San Juan Co., mouth of Castle Creek, along San Juan River, *Adams 2165/B9793* (MNA). Sanpete Co., Maroni, *Eastwood & Howell 596* (CAS). Uintah Co., 3 mi. SE of Pelican Lake, Ouray Nat'l. Wildlife Refuge, *Neese & Neese 7571* (BRY); E of Jensen, *Osterhout 6424* (RM, 2 sheets).

Plants of this distinctive subspecies typically grow at xeric sites in heavy clays, sandstones, or gypsum soils and are characterized by often dense, soft, white, crinkly villous pubescence, and quadrangular capsules with distinct cross-veins, a typically truncate base, conspicuous abruptly constricted sterile beak, and valves that remain erect or are incurved after dehiscence. They also usually have leaves with a rhombic terminal portion and buds that sometimes nod somewhat prior to anthesis. Munz (1931b) based *Oenothera caespitosa* var. *jonesii* in part on plants of *O. caespitosa* subsp. *navajoensis*. The type and only fruiting specimen that Munz saw of what he named *O. caespitosa* var. *jonesii* is, unfortunately, material of *O. caespitosa* subsp. *crinita* from the Fish Springs in Juab County, Utah, and not from the Fish Springs in Grand County, Utah, as Munz thought. None of the other three collections, all of *O. caespitosa* subsp. *navajoensis*, that Munz cited (1931b), had mature fruit. His concept of *O. caespitosa* var. *jonesii* was based, therefore, on the possession of dense pubescence, rhombic-obovate leaves, and terete, ovoid capsules, the last feature, of course, seen only in the type. Both *O. caespitosa* subsp. *navajoensis* and subsp. *crinita* sometimes have these leaf and hair features but only the latter has terete ovoid capsules. Thus Munz excluded all fruiting material of *O. caespitosa* subsp. *navajoensis* that he saw from var. *jonesii*, even when it was extremely similar in leaf and hair characters to material he did include [e.g., 1911, *Standley s.n.*, Carrizo Mts., Apache Co., Arizona (GH); 1914, *Jones s.n.*, LaSal Mts., Grand Co., Utah (POM); 1883, *Jones s.n.*, Grand Junction, Mesa Co., Colorado (POM)]. He placed all of these collections in his "dustbin" taxon, *O. caespitosa* var. *montana*. Judged from Munz's annotations after 1931, it is apparent that he had considerably broadened his concept of var. *jonesii* so that it was roughly parallel to our concept of subsp. *navajoensis*.

Only one plant, from a population at Blue Notch, a monument rock near Lake Powell, *Stockhouse 547*, was tetraploid with configurations ranging from 14 bivalents to seven bivalents plus one univalent, two quadrivalents, and one pentavalent. Pollen fertility of this plant was low, with ca. 25% pollen stainability (Stockhouse, 1973). This plant was most likely of spontaneous autopolyploid origin. Four other populations, three from adjacent Grand County, Utah and one other from the Lake Powell area, were all diploid.

As is the case with the other subspecies of *Oenothera caespitosa*, subsp. *navajoensis* has considerable morphological variation among and often within populations. Some of this variability can probably be explained by past and present hybridization with *O. caespitosa* subsp. *marginata*. Plants with small leaves and capsules and often dense pubescence are common from the drier interior and southern portions of the Colorado Plateau, while plants with stems often up to 2.5 dm long tend to occur more commonly in the moister climate along the periphery of the region. The predominance of short-caulescent and acaulescent collections in herbaria is misleading, because plants are typically collected during the major part of the flowering period when they are most conspicuous, but before the stems elongate, as they do subsequently in many plants. For this reason, it is difficult to know the exact distribution of caulescent plants. Less clearly related to edaphic or climatic adaptation are the nearly linear-leaved but pinnately lobed plants of subsp. *navajoensis* from Sevier County, Utah. Some of these plants have pinnately lobed leaves over 17 cm long, and thus approach subsp. *marginata*. Judged from their intermediate habitat, which approaches that of subsp. *marginata*, it is likely that at least these plants are hybrids or hybrid derivatives, and they are discussed in the appendix. Other populations, however, also have pinnately lobed leaves, but grow in typical clay or gypsum habitats in low elevation xeric scrub communities (e.g., *Wagner 4511*, Mesa Co., Colorado). Most morphological features of those

FIGURE 106. *Oenothera caespitosa* subsp. *macroglottis*; Grand Co., Colorado, *Dress 9151* (BH).

plants are within the normal range of variation of subsp. *navajoensis* and do not otherwise resemble subsp. *marginata*.

1d. Oenothera caespitosa Nutt. subsp. **macroglottis** (Rydb.) W. L. Wagner, Stockhouse, & Klein in Wagner, Ann. Missouri Bot. Gard. 70: 195. 1983. *Pachylophus macroglottis* Rydb., Bull. Torrey Bot. Club 30: 259. 1903. TYPE: "Turkey Creek and tributaries," in present vicinity of Veta Pass, Huerfano Co., Colorado, 2,800–2,900 m, 8–9 June 1900, *Rydberg & Vreeland 5857* (holotype, NY, photo MO; isotype, RM). (Locality reconstructed with the aid of R. Barneby, pers. comm.) Woot. & Standl., Contr. U.S. Natl. Herb. 19: 471. 1915. Rydb., Fl. Rocky Mts. 598. 1922. Tidestrom, Contr. U.S. Natl. Herb. 25: 380. 1925. Figure 106.

Pachylophus hirsutus Rydb., Bull. Torrey Bot. Club 31: 571. 1904. TYPE: Georgetown, Clear Creek Co., Colorado, 18 Aug. 1895, *Rydberg* (holotype, NY, photo MO).

Pachylophus caulescens sensu Woot. & Standl., Contr. U.S. Natl. Herb. 19: 471. 1915, non Rydb.

Oenothera caespitosa var. *montana* sensu Munz, Amer. J. Bot. 18: 732. 1931, pro parte, non (Nutt.) Durand. Harrington, Man. Pl. Colo. 396. 1954. Martin & Hutchins, Fl. N. M. II: 1390. 1981, pro parte. *Oenothera caespitosa* subsp. *montana* sensu Munz, N. Amer. Fl., Ser. II, 5: 101. 1965, pro parte, non (Nutt.) Munz.

Acaulescent perennial herb or rarely with a short congested stem 4–8 cm long from a stout somewhat fleshy to woody taproot, often adventitious shoots are produced from spreading lateral roots, rosettes densely leafy; stems, if present, simple or rarely with 1 to several short laterals. Leaves dark green, often lustrous, the veins paler, moderately thick and usually semi-succulent, often undulate, hirsute mostly along the margins and primary veins, the hairs 0.4–1.6 mm long, mixed with minute glandular hairs 0.14–0.18 mm long, sometimes glabrous, oblan-

ceolate to spatulate, (6.8–)9.5–23(–32) cm long, (1.3–)2.4–4.5(–6.5) cm wide, apex acute to rounded, rarely acuminate, regularly to irregularly dentate, usually 1–3 small teeth, 1–2 mm high between each pair of larger teeth, 3–4 mm high, sometimes with a few larger lobes toward the base, rarely the blade coarsely and irregularly pinnately-lobed, gradually tapering to a petiole (3–)4–11(–14) cm long. Buds erect. Flowers 1–2(–4) opening per day. Ovary glandular pubescent, typically hirsute, sometimes glabrous, (14–)16–22(–28) mm long on a short pedicel 1–3 mm long. Floral tube (4.5–)7.5–11(–15.3) cm, 1.5–2.5 mm diam. medially, flaring to (9–)12–23 mm at the mouth, hirsute and glandular pubescent or glabrous. Sepals green, the veins infused with rich reddish purple pigment, (2.2–)3–4.5(–5) cm long, (3–)5–8 mm wide, pubescence the same as the floral tube, although usually more densely hirsute along the midveins, or glabrous. Petals fading pink to pale rose, (2.1–)3.5–4.3(–5) cm long, (2.4–)4.5–6(–6.8) cm wide, the notch broad 6–10(–12) mm long, subglabrous. Staminal filaments (16–)19–28(–35) mm long; anthers (10–)12–17 mm long. Style 8.5–18 cm long; stigma lobes (4–)6–12 mm long. Capsules 2–4(–8) maturing, lance-cylindrical to cylindrical, somewhat curved, rounded in cross-section, symmetrical throughout or occasionally asymmetrical at the base by being slightly flattened on one side, (1.7–)2.5–4.5(–5.6) cm long, 5–8 mm diam., tapering to a sterile beak 6–15 mm long, the free tips 1–4 mm long, usually recurved, hirsute and glandular pubescent becoming glabrate in age, the margins of the valves with a conspicuous nearly smooth to irregular undulate ridge, ca. 1.5 mm high, the cross-veins visible but not conspicuous, the base short attenuate to cuneate, length of dehiscence ½–⅔ capsule length, the valves spreading; pedicel 2–7 mm long. Seeds 80–140 per capsule in two adjacent and distinct rows in each locule, the raphe parallel to the plane of the capsular axis, narrowly obovoid, usually straight, light brown to dark reddish brown, 2.5–3 mm long, 1–1.4 mm wide, 1.2–1.6 mm high; embryo portion constituting ca. ½ of the seed volume, the surface minutely papillose; seed-collar forming a narrow slit above the raphe with a slightly sunken membrane, the margin entire or obscurely sinuate distally, the surface reticulate to papillose, the papillae low and broad, not collapsed. Gametic chromosome numbers, $n = 7, 14$.

Distribution (Fig. 107). On open igneous rocky slopes, talus, roadcuts, open or shaded and sandy or gravelly sites along streams, rarely on shale, in upper pinyon-juniper woodland and Gambel oak scrub through ponderosa pine forest, ponderosa pine-Douglas fir forest to spruce-fir-lodgepole pine forest, from southeastern Wyoming through the southern Rocky Mountains in Colorado and northern New Mexico with disjunct populations in the LaSal and Abajo Mountains in southeastern Utah and Sandia and Manzano Mountains of central New Mexico, 2,000–3,050 m. Flowering from late May through July.

Representative specimens examined. UNITED STATES. COLORADO: Alamosa Co., Great Sand Dunes Nat'l. Monument, *Stockhouse 147* (MO). Archuleta Co., Arboles, *Baker 496* (BM, E, F, G, GH, MO, NDG, NMC, NY, POM, RM, US). Boulder Co., 7 mi. E of Ward, Left Hand Canyon, *Goeken 20* (CS); 1.4 mi. E of Nederland, Hwy. 119, *Stockhouse 120* (MO); 10 mi. W of Boulder on Hwy. 119, *Stockhouse 123* (MO); 3.8 mi. W of jct. Hwy. 36 & 7, slopes along St. Vrain Creek, *Wagner 4023* (MO). Chaffee Co., Poncha Springs, rd. to Monarch Pass, *Dunn 15420* (KANU, UMO). Clear Creek Co., near Georgetown, 1885, *Patterson s.n.* (F, MIN). Conejos Co., San Luis Valley, Alamosa Canyon, *Ramaley 15815* (COLO). Costilla Co., La Veta Pass, *McKelvey 193* (GH). Custer Co., 18 mi. E of Westcliffe on Rt. 96, *Goeken 17* (CS). Dolores Co., Dolores along RR, *Crandall 1527* (CS). Delta Co., Surface Creek, *Camp & Camp 41086* (MICH). Douglas Co., Palmer Lake, 1883, *Woodward s.n.* (YU). Eagle Co., Minturn, *Osterhout 2546* (POM, RM). El Paso Co., Cross Ruxton, *Clements & Clements 106* (CU, DAO, DS, E, G, MIN, NY, RM, US); Monument Lake, *Nelson 4620* (DS, MO, RM, US); 5 mi. up Rampart Range Rd. from Garden of the Gods. *Stockhouse 115* (MO); 8 mi. up Rampart Range Rd. from Garden of the Gods, *Stockhouse 116* (MO); Gold Camp Rd., Bear Creek Canyon, *Stockhouse 118* (MO). Fremont Co., S of Canyon City, Cow Creek, *Ewan 14231* (CAS, COLO, NA, RSA). Garfield Co., Elk Canyon, *Crandall 1300* (CS, RM, WS, YU). Grand Co., Hwy. 125, Arapahoe Nat'l. Forest, *Dress 9151* (BH). Gunnison Co., Cerro Summit, *Baker 172* (E, G, GH, MIN, MO, NDG, NY, POM, RM). Hinsdale Co., 3 mi. S of Lake City, *Beaman & Erbisch 1109* (RM). Huerfano Co., 9 mi. SW of Cuchara, *Stephans & Brooks 22135* (DS, KANU). Jackson Co., 1 mi. NE of Rand, *Stockhouse 527* (MO). Jefferson Co., Hwy. 72, 5 mi. NW of Coal Creek, *Klein 1490* (RSA, UC). Lake Co., W of Twin Lakes, *Raven 26548* (MO). La Plata Co., 2.5 mi. W of Archuleta Co. line, along Hwy. 160, *Wagner 4514* (MO). Larimer Co., Poudre Canyon, *Goeken 1* (CS); W of Bellvue, Rist Canyon Rd., *Klein 1112* (RSA); 3.5 mi. W of Bellvue, *Stockhouse 114* (MO); 14.2 mi. S of jct. Hwy. 14 along road to Pingree Park, *Stockhouse 119* (MO). Las Animas Co., foothills near Dix, 1898, *Baker et al. s.n.* (MO, NY, POM). Mesa Co., Colorado Nat'l. Monument, S of Fruita, *Weber 3883* (ARIZ). Mineral Co., Rio Grand Nat'l. Forest, Wagon Wheel Gap Exp. Sta.,

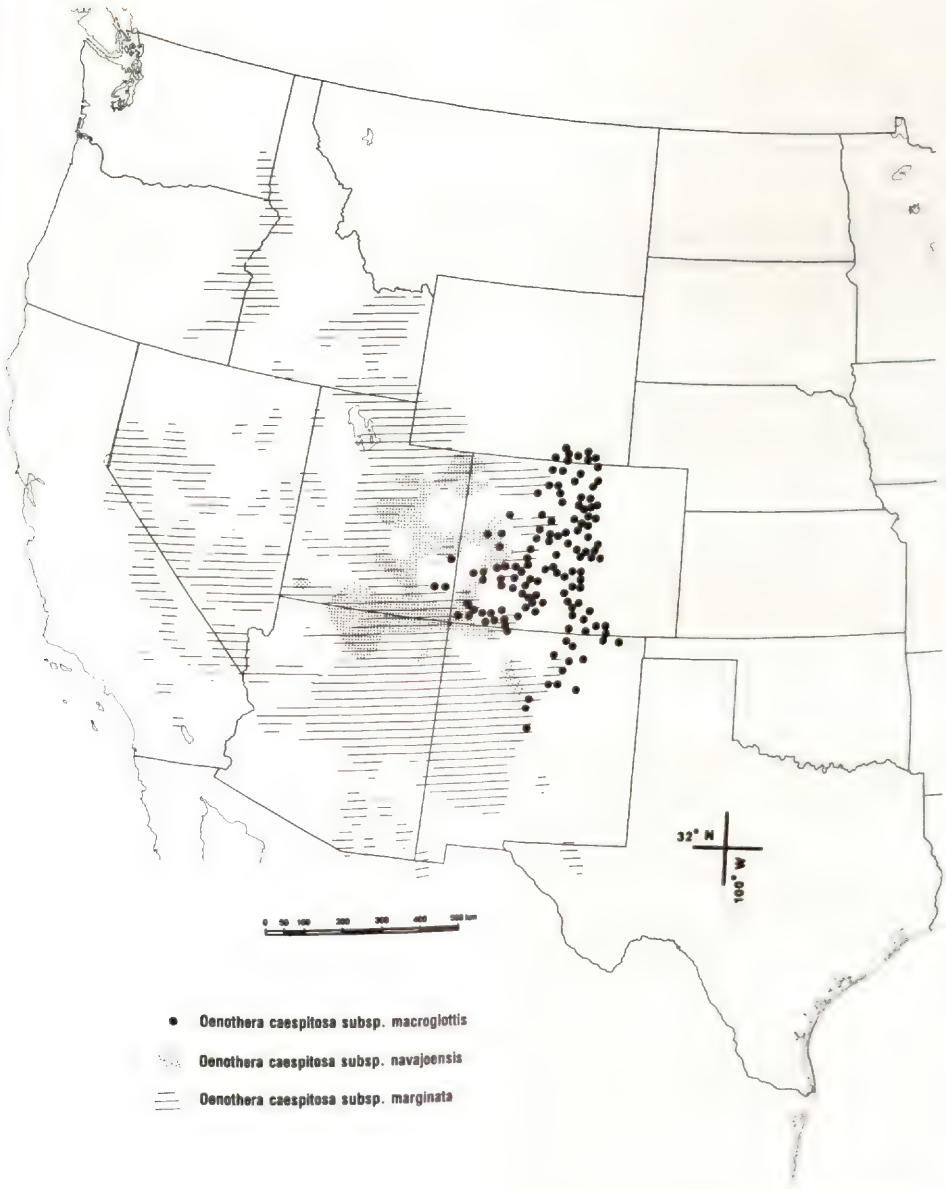

32° N
100° W
0 50 100 200 300 400 500 km
Oenothera caespitosa subsp. macroglottis
Oenothera caespitosa subsp. navajoensis
Oenothera caespitosa subsp. marginata

FIGURE 107. Distribution of *Oenothera caespitosa* subsp. *macroglottis* relative to the distribution of *O. caespitosa* subspp. *marginata* and *navajoensis*.

Murdoch 4551 (F, GH, MO, NY, UC, US). Montezuma Co., Mancos, *Baker et al. 141* (BM, CS, CU, E, F, G, GH, MICH, MIN, MO, NDG, NY, POM, RM, US). Montrose Co., Naturita, *Payson 311* (COLO, GH, MO, RM). Ouray Co., 4 mi. N of Ouray, *Raven 13040* (NY, RSA, UC, UT). Park Co., South Park, *Wolf 132* (CU, F, MICH, NY). Pitkin Co., 1 mi. below Aspen Airport, *Raven 26537* (MO). Rio Grande Co., Del Norte, *Ramaley & Johnson 14558* (COLO). Routt Co., 0.9 mi. N of Oak Creek, *Wagner 4041* (MO). Saguache Co., Monarch Pass, *Dziekanowski 871* (UMO); 2 mi. S of O'Haver Lake turnoff, Poncha Pass, *Goeken 11*

(CS). San Miguel Co., 1.5 mi. S of jct. S-145 & 145, *Stockhouse 172* (MO); Norwood Hill, *Walker 485* (BH, E, GH, MIN, RM, US, WS). Summit Co., 11.7 mi. N of Rock Creek, *MacCreary 86* (CS). Teller Co., Manitou, *Coulter 5804* (F); Woodland Park, 1926, *Kraus s.n.* (WIS); 4 mi. W of Florissant, *Stockhouse 110* (MO). Weld Co., S St. Vrain Canyon, 1928, *Ricket s.n.* (UMO). NEW MEXICO: Bernalillo Co., 1 mi. S of Sandia Crest on Crest Trail, *Martin 4143* (MO, UNM). Colfax Co., Johnson Mesa, *Nelson & Nelson 4694* (DS, GH, RM, UC). Rio Arriba Co., Rosa, *Flowers & Hall 28* (UT). San Miguel Co., Holy Ghost Creek, 1908, *Standley s.n.* (GH, MO, NMC, NY). Santa Fe Co., Santa Fe Canyon, *Heller & Heller 3773* (MO). Taos Co., E of Red River, *Clark 16065* (UNM). San Juan Co., Aztec Ridge, 1898, *unknown collector s.n.* (SD). Torrance Co., Manzano Mts., Capillo Peak, *Dunn 6327* (DAO, UMO). Union Co., Capulin Mts., *Waterfall 10843* (COLO, RSA, UTC). UTAH: San Juan Co., LaSal Mts., 4 mi. up Geyser Pass, *Pederson 95* (UT); Abajo Mts., 14 mi. W of Monticello, Blue Creek, *Stockhouse 537* (MO); LaSal Mts., Geyser Reservoir, *Walker 251* (BH, E, GH, MIN, NY, RM, US, WS). WYOMING: Albany Co., Centennial Hills, *Nelson 1274* (CU, GH, MIN, MO, NY). Carbon Co., Six Mile Gap, North Platte River, *Nelson & Nelson 428* (RM). Laramie Co., 20 mi. W of Cheyenne on I-80, *Wagner 4030* (MO).

The plants treated here as *Oenothera caespitosa* subsp. *macroglottis* were included by Munz (1931b) within his broadly defined *O. caespitosa* var. *montana*. Munz included plants from all subspecies recognized in this treatment in that taxon. These inclusions were a major factor in leading him to believe erroneously that *O. caespitosa* was made up of broadly sympatric and freely intergrading, modally distinctive varieties. In the present treatment the type of *O. montana* and many of the collections Munz placed in his var. *montana* are included under *O. caespitosa* subsp. *caespitosa*, with most of the remainder assigned to subsp. *macroglottis*, but also with a few collections included under subspp. *marginata, navajoensis*, and *crinita*.

The slightly curved, large capsules with their unique undulate ridges along the valves, coarsely dentate spatulate to broadly oblanceolate leaves, widely flaring floral tubes (commonly 1–2 cm wide at the mouth), papillose seeds with noncollapsed papillae and an inflated collar, and cool montane habitat clearly set *Oenothera caespitosa* subsp. *macroglottis* apart from other taxa in the group.

Oenothera caespitosa subsp. *macroglottis* is extremely variable in certain characters. Perhaps the most conspicuously variable feature is the length of the floral tubes, which ranges from 4.5 to over 15 cm. Nearly the full range of this variability can be found within many individual populations. There is, however, a minor geographical trend: populations from central and western Colorado localities have mean floral tube lengths from 7.3–8.5 cm whereas populations from the Front Range in Colorado southward to northern New Mexico have longer mean tube lengths, mostly from 9–11 cm. In addition to this geographical pattern there are two other components to the overall pattern of variation. First, there is a tendency for individual plants to produce flowers with shorter tubes both early and late in the flowering season. Secondly, plants in more xeric sites tend to have shorter tubes, a relationship that may in part represent phenetic plasticity. Similarly variable floral tubes are found in the closely related, *O. caespitosa* subsp. *marginata* as well as in the unrelated *O. brachycarpa* A. Gray (sect. *Megapterium*), *O. flava* (A. Nels.) Garrett (sect. *Lavauxia*), and several other long floral-tubed species distributed in other sections.

Clearly, evolution of longer floral tubes in *Oenothera* is an adaptation to pollination by long-tongued hawkmoths such as species of *Sphinx* and *Manduca* (Gregory, 1964) and has evolved independently in many sections of the genus. Selection for longer floral tubes, however, has not precluded these flowers from continued visitation and effective pollination by shorter-tongued moths such as *Hyles* and some species of *Sphinx* (Gregory, 1964).

Some plants of *Oenothera caespitosa* subsp. *macroglottis*, especially from the southern portion of its range, are densely hirsute, especially on the young leaves, buds, and floral tubes. It was on one of these plants that Rydberg based the name *Pachylophus hirsutus*. At the opposite extreme there are striking plants scattered throughout the northern and eastern portion of the range that are only glandular-pubescent or glabrous. These plants typically grow intermixed with sparsely and more densely hirsute plants (e.g., Teller Co., Colorado, 1926, *Kraus s.n.*; Lake Co., Colorado, *Raven 26548*; San Miguel Co., Colorado, *Stockhouse 172*). Since the lack of one or both hair types and the increased density of the hirsute type have apparently evolved independently on several occasions and occur mixed in populations with less extreme individuals, neither warrants any formal taxonomic recognition. The trends to denser pubescence or to the loss of hirsute pubescence may be responses to moister or drier sites, respectively. Likewise, the extreme variation in leaf length may be primarily a response to site conditions.

Tetraploid populations are known from El Paso, Teller, Saguache, and Summit Counties, Colorado. These plants are morphologically indistinguishable from diploid individuals of this subspecies. They are restricted to the east central part of the range of the subspecies. A more extensive sample is needed to determine whether the plants throughout this geographical area are exclusively tetraploid or whether tetraploid plants occur elsewhere. Plants with irregularly deeply pinnate lobes on the leaves and huge buds with petals over 6 cm long grow near Monument Lake, El Paso County, Colorado, *Nelson & Nelson 4620*; their chromosome number should be investigated also.

Disjunct populations of *Oenothera caespitosa* subsp. *macroglottis* occur in the Abajo and LaSal Mountains in southeastern Utah; the Sandia Mountains, Bernalillo County, in central New Mexico; and also ca. 50 km farther south in the Manzano Mountains, Torrance County, New Mexico. Judged from the low dispersibility of *O. caespitosa* and the fact that populations are restricted to higher elevations in cool mesic conifer forests, these populations are presumed to be relicts from the last glacial period rather than ones resulting from recent dispersal events. Many of these plants have atypical and unique deeply pinnately lobed leaves and are densely hirsute (e.g., *Martin 4143*, Bernalillo Co., New Mexico; and *Pederson 95*, San Juan Co., Utah).

1e. Oenothera caespitosa Nutt. subsp. **marginata** (Nutt. ex Hook. & Arn.) Munz, N. Amer. Fl., Ser. II, 5: 101. 1965. Beatley, Vasc. Pl. Nev. Test Site & Cent. S. Nev. 219. 1976. *Oenothera marginata* Nutt. ex Hook. & Arn., Bot. Beechey Voy. 342. 1839. TYPE: Salmon Falls of Snake River, Twin Falls Co., Idaho, summer of 1837, *Tolmie 45* (lectotype here designated, K, photo MO; probable isolectotype, E). The collection was actually made by a friend of Mr. Tolmie's, John McLeod, who collected some 70 specimens for Tolmie while conducting a party of trappers to the rendevous of the American trappers in the Green River Valley, Wyoming (McKelvey, 1955: 627–635). This collection is clearly the type rather than the Nuttall collection mentioned by Munz (1931b, 1965). The material now in the Hooker Herbarium, which was forwarded to Hooker by Tolmie, is a mixture of *O. caespitosa* subspp. *marginata* and *caespitosa*, but Hooker's description stating that the plants have spreading villous hairs and dentate-pinnatifid leaves clearly describes the material of subsp. *marginata*, while it does not at all fit the specimens of subsp. *caespitosa* with their mostly appressed pubescence and entire leaves. Torr. & A. Gray, N. Amer. Fl. 1: 500. 1840. Tidestrom & Kittell, Fl. Ariz. N. M. 276. 1941. *Pachylophus marginatus* (Nutt. ex Hook. & Arn.) Rydb., Bull. Torrey Bot. Club 33: 146. 1906; Fl. Rocky Mts. 598. 1922. Tidestrom, Contr. U.S. Natl. Herb. 25: 380. 1925. *Oenothera caespitosa* Nutt. var. *marginata* (Nutt. ex Hook. & Arn.) Munz, Amer. J. Bot. 18: 733. 1931, pro parte. Abrams, Illus. Fl. Pac. States 3: 195. 1951. Clokey, Univ. Calif. Publ. Bot. 24: 158. 1951. Patraw, Fl. Southw. Mesas 30. 1951. Davis, Fl. Id. 497. 1952. Harrington, Man. Pl. Colo. 396. 1954. Munz, Calif. Fl. 949. 1959, pro parte. Kearney & Peebles, Ariz. Fl. Ed. 2, 598. 1960. Hitchcock et al., Vasc. Pl. Pac. Northw. 495. 1961. Peck, Man. High. Pl. Ore. Ed. 2, 544. 1961. St. John, Fl. Southe. Wash. Ed. 3, 302. 1963. McDougall, Grand Can. Wildfl. 163. 1964. Wiggins, Fl. Sonoran Desert 2: 1051. 1964. Rickett, Wildfl. U.S. Southw. States 4(2): 321. pl. 105. 1970. Hitchcock & Cronquist, Fl. Pac. Northw. 310. 1973. Lloyd & Mitchell, Fl. White Mts. Calif. Nev. 114. 1973. McDougall, Seed Pl. N. Ariz. 334. 1973. Munz, Fl. S. Calif. 613. 1974, pro parte. Nelson, Pl. Zion Natl. Park 180. fig. 125. 1975. Lehr, Cat. Fl. Ariz. 109. 1978. Martin & Hutchins, Fl. N. M. II: 1388. 1981, pro parte. Figure 108.

Oenothera eximia A. Gray, Mem. Amer. Acad. Arts n.s. 4: 45. 1849. TYPE: Santa Fe Creek, Santa Fe Co., New Mexico, June–July 1847, *Fendler 228* (holotype, GH, photo MO; isotypes, GH, MO, UC). Gray's description is clearly based on one of the sheets at GH and it is considered to be the holotype. Tidestrom & Kittell, Fl. Ariz. N. M. 277. 1941, pro parte. *Pachylophus exiguus* (A. Gray) Rydb., Bull. Torrey Bot. Club 30: 260. 1903, pro parte. An error by Rydberg based on *O. eximia* A. Gray. *Pachylophus eximius* (A. Gray) Woot. & Standl., Contr. U.S. Natl. Herb. 19: 471. 1915, pro parte; Rydb. Fl. Rocky Mts. 598. 1922, pro parte; Fl. Plains N. Amer. 576. 1932, pro parte. *Oenothera caespitosa* Nutt. var. *eximia* (A. Gray) Munz, Amer. J. Bot. 18: 731. 1931, pro parte. Munz in Lundell, Tex. Fl. 239. 1944. Harrington, Man. Pl. Colo. 396. 1954, pro parte. Raven in Correll & Johnston, Man. Vasc. Pl. Tex. 1130. 1970. *Oenothera caespitosa* Nutt. subsp.

FIGURE 108. *Oenothera caespitosa* subsp. *marginata*; Coconino Co., Arizona, *Peebles & Smith 13953* (ARIZ).

eximia (A. Gray) Munz, N. Amer. Fl., Ser. II, 5: 100. 1965.

Oenothera idahoensis Mulford, Bot. Gaz. (Crawfordsville) 19: 117. 1894. TYPE: Curlew Gulch beyond Boise City, Ada Co., Idaho, 15 June 1892, *Mulford s.n.* (lectotype, GH; isolectotypes, GH, MO, NY; Munz, Amer. J. Bot. 18: 734. 1931).

Anogra longiflora Heller, Muhlenbergia 2: 224. 1906. TYPE: Silver Canyon opposite laws, Inyo Co., California, 9 May 1906, *Heller 8219* (lectotype here designated, DS-29366; isolectotypes, CAS, DS, E, F, MO, NY, PH, US). *Pachylophus longiflorus* (Heller) Heller, Muhlenbergia 4: 40. 1908. *Oenothera caespitosa* Nutt. var. *longiflora* (Heller)

Munz, Amer. J. Bot. 18: 734. 1931. Abrams, Illus. Fl. Pac. States 3: 195. 1951. Munz, Calif. Fl. 950. 1959. Kearney & Peebles, Ariz. Fl. Ed. 2, 598. 1960.

Pachylophus cylindrocarpus A. Nels., Bot. Gaz. (Crawfordsville) 47: 429. 1909. TYPE: Carson's Meadow Valley Wash, Lincoln or Clark Co., Nevada, 26 May 1904, *Goodding 960a* (holotype, RM-42165, photo MO; isotype, RM).

Pachylophus hirsutus sensu Woot. & Standl., Contr. U.S. Natl. Herb. 19: 471. 1915, non Rydb.

Pachylophus prolatus A. Nels., Amer. J. Bot. 25: 114. 1938. TYPE: Globe, Gila Co., Arizona, 4 May 1925, *Nelson 10300* (lectotype, here designated, RM-138739; isolectotype, RM).

Oenothera caespitosa var. *montana* sensu Kearney & Peebles, Ariz. Fl. Ed. 2, 598. 1960, pro parte, non (Nutt.) Durand. Martin et al., Fl. Sandia Mts., N. M. Ed. 2, 176. 1971. Hitchcock & Cronquist, (Fl.) Pac. Northw. 310. 1973, pro parte. McDougall, Seed Pl. N. Ariz. 334. 1973, pro parte. Hutchins, Fl. White Mt. Area N. M. 342. 1974. Lehr, Cat. Fl. Ariz. 109. 1978, pro parte. Martin & Hutchins, Fl. N. M. II: 390. 1981, pro parte.

Generally robust caulescent and caespitose to acaulescent perennial herb from a stout often somewhat fleshy taproot; stems 1–4 dm long, ascending to decumbent from a densely leafy rosette, 1–8(–15) secondary branches arising near the base, straw-colored or sometimes reddish purple, moderately to densely hirsute, the hairs stiffly erect (0.3–)0.5–2.2 mm long and often variable on any one individual mixed with minute glandular hairs, 0.14–0.2(–0.25) mm long, rarely plants only glandular. Leaves grayish green to green sometimes with scattered reddish purple splotches on the upper surface, moderately to densely hirsute and glandular, rarely only the glandular hairs present, sometimes both types of hairs more restricted to the margins and major veins, oblanceolate to narrowly elliptic, rarely lanceolate, (2.8–)10–26(–36) cm long, (0.6–)1–3(–4.5) cm wide, acute to rounded at the apex, coarsely and irregularly pinnately-lobed to dentate or rarely serrate, the lobes rarely cut more than halfway to the midrib, sometimes only coarsely erose, the lobes narrow to broadly triangular or oblong, acute, the smaller ones 0.3–2 mm high, the larger 4–8 mm high, gradually tapering to a long petiole (3–)4–11(–14) cm long. Buds erect. Flowers 1–4(–10) per stem opening per day. Ovary (11–)20–32(–39) mm long, sessile or on a pedicel 3–30 mm long, densely glandular and often hirsute, sometimes (Arizona) the larger hairs with a reddish purple pustulate base. Floral tubes (4.1–)8–14(–16.5) cm long, 1.5–2.2 mm diam. medially, flaring to 7–12(–14) mm at the mouth, hirsute and/or glandular pubescent, rarely subglabrous. Sepals green, the veins infused with reddish purple pigment, sometimes also with reddish purple splotches, (2.2–)3.4–4.5(–5.4) cm long, (4–)5–8(–9) mm wide, pubescence the same as the floral tube, usually more densely hirsute along the midvein. Petals fading pink to lavender, (2.4–)3.5–5(–6) cm long, (2.8–)4–6.3(–7) cm wide, the notch 6–8(–10) mm deep, subglabrous. Staminal filaments (16–)20–30(–35) mm long; anthers (10–)12–17(–20) mm long. Style (7.8–)10–15(–18.5) cm long; stigma lobes (5–)6–8(–10) mm long. Capsule (1–)3–15 rarely more maturing per stem, cylindrical to sometimes lance-cylindrical, rounded to obtusely quadrangular in cross-section, straight and nearly symmetrical and obtuse to cuneate at the base, (2.1–)2.5–5(–6.8) cm long, 6–8 mm diam., tapering to a short sterile beak 2–10(–12) mm long, the free tips 1.5–4 mm long spreading to recurved, hirsute and/or glandular pubescent, sessile or on a pedicel 1–40(–55) mm long, the margins of the valves with minute to conspicuous tubercles, these sometimes coalesced into a sinuate-ridge, the tubercles 0.3–2 mm high, 1–4.5 mm apart, the cross-veins prominent to obscure, dehiscing ½–⅞ their length, the valves spreading. Seeds 75–170 per capsule, in two partially overlapping rows or rarely only one irregular row in each locule, the raphe oblique to the plane of the capsular axis, narrowly to broadly obovoid rarely nearly orbicular, nearly straight, light to dark brown, 2.2–3.4 mm long, 1.1–2.6 mm wide, 1.5–2.2 mm high; embryo portion constituting about ⅛–½ of seed volume, the surface appearing longitudinally striate, reticulate under magnification; seed-collar large and usually appearing inflated, sealed by a flat membrane which is often slightly depressed into the seed-collar cavity, the margin entire to obscurely sinuate distally, the surface smooth to finely striate. Gametic chromosome number, $n = 7$.

Distribution (Fig. 109). On rocky slopes, cracks in rocks, talus, along gravelly creek beds and arroyos, or roadcuts in loose to somewhat compacted soils derived from granite, sandstones, limestone, volcanic cinders, or rarely shale; mostly in foothill communities of pinyon-juniper woodland, big sagebrush scrub, Arizona chaparral, grasslands to higher elevations in opening in ponderosa pine forest, rarely at higher elevations ranging from extreme eastern Washington, eastern Oregon, and adjacent Idaho, south to western Colorado, all but the eastern plains of New Mexico to the Guadalupe Mountains of

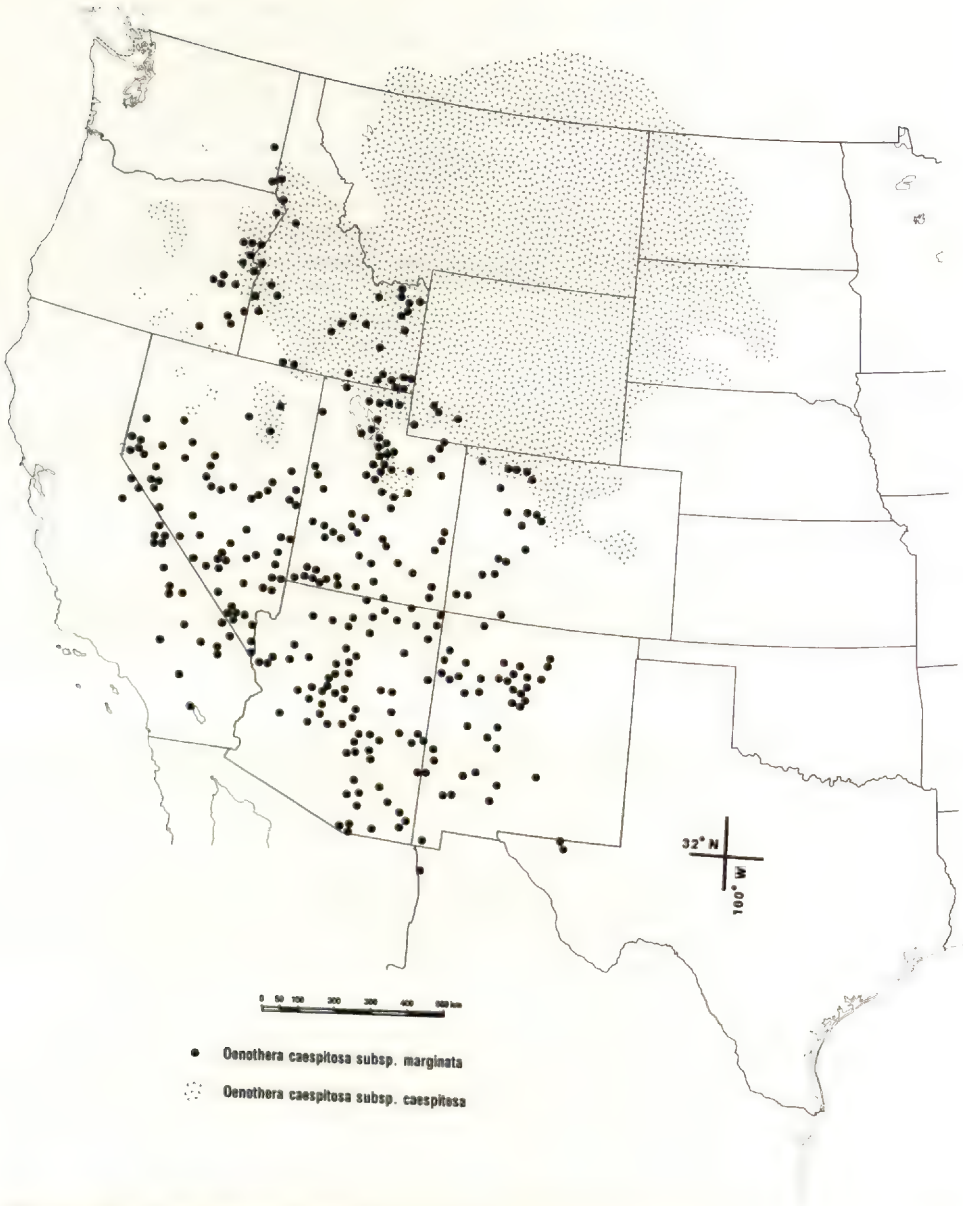


FIGURE 109. Distribution of *Oenothera caespitosa* subsp. *marginata* relative to that of *O. caespitosa* subsp. *caespitosa* (shaded).

Trans-Pecos Texas and Carretas, Chihuahua, throughout Arizona except the Sonoran Desert and east to the Santa Rosa, White and San Bernadino Mts. and the east slope of the Sierra Nevada near Pinto Creek of the Inyo region, California, (450–)1,200–2,300(–3,050) m. Flowering from mid-March to July.

A collection said to be from the Rough and Ready Desert, Josephine County, southwestern Oregon, 1940, *Gilkey s.n.* (OSC-96578), is doubtfully from this locality. The species is otherwise unknown from west of the Cascades. Another questionable record is one from gypsum soils of Commanche Bluffs, 11 km E of Roswell,

Chaves County, New Mexico, *Sears 1656* (BRY). Other than this collection, *O. caespitosa* subsp. *marginata* is known in southeastern New Mexico only from a few scattered and presumably relict populations in woodland to forest vegetation in the Sacramento and the Guadalupe Mountains, just over the New Mexico border in Texas. All of these populations are above 2,100 m, whereas the Commanche Bluff area is in the Chihuahuan Desert at only ca. 1,100 m. It seems most unlikely that the label data on this collection are correct, but this locality should be investigated.

Representative specimens examined. MEXICO. CHIHUAHUA: Sierra Madre, 1869, *Anderson s.n.* (MO); Carretas, *White 2577* (ARIZ, GH, MICH). SONORA: Los Nogales, *Smith s.n.* (NY). UNITED STATES. ARIZONA: Apache Co., N end of Carrizo Mts., 1911, *Standley s.n.* (GH, MO, NY); 2 mi. N of Mexican Hay Lake on Hwy. 273, *Wagner 3794* (MO). Cochise Co., E of Wilcox, 1919, *Goodding s.n.* (DS, MNA, NY). Coconino Co., Grand Canyon, Point Sublime, *Gregory 433* (CAS, RSA, UC); Grand Canyon, Kaibab Trail, *Gregory 435* (CAS, DAO, DS, RSA, US); 3 mi. E of Jacobs Lake, *Gregory 437* (CAS, DS, RSA, UC); S end of Navajo Mt., *Peebles & Smith 13953* (ARIZ); jct. Lake Mary Rd. and I-17, near Flagstaff, *Wagner 3793* (MO). Gila Co., Salt Gulch, Lake Roosevelt, *Fletcher 4241* (MO). Greenlee Co., N of Clifton, *Davidson 243* (DS). Graham Co., Cedar Spring, *Toumey 133½* (ARIZ). Maricopa Co., Apache Trail, Fish Creek Hill, *Gillespie 5569* (BH, GH, POM, UC). Mohave Co., Grand Canyon, Toroweap Valley, *McClintock 52-450* (ARIZ, CAS, NY, WS). Navajo Co., Navajo Nat'l. Monument, *Skougard & Nebeker 194* (BRY). Pima Co., Santa Catalina Mts., above Prison Camp, *Parker 7444* (ARIZ, MO, NY, RSA, US, WS). Pinal Co., 8.1 mi. S of Oracle, road to Mt. Lemmon, *Lehto et al. 11000* (ASU, NY, US, WTS). Santa Cruz Co., 8 mi. SE of Arivaca, *Holmgren & Holmgren 6831* (ASU, NY, RENO, US); Ruby to Nogales, *Peebles & Fulton 11448* (ARIZ, F, POM, US). Yavapai Co., Perkinsville, *Demaree 43941* (ARIZ, ASC, RSA). Yuma Co., Mt. Harguahala, 1922, *Moore s.n.* (US). CALIFORNIA: Inyo Co., White Mts., Black Canyon, *Duran 552* (ARIZ, BM, CAS, CU, DS, E, F, G, LA, MICH, MIN, MO, NY, POM, RM, SD, UC, UTC, WIS); Inyo Mts., 5.5 mi. W of Westgard Pass, *Gregory 391* (CAS, RSA, UC), *Gregory 392* (RSA, UC). Mono Co., Topaz Lake, *Klein 416* (RSA). Riverside Co., Santa Rosa Mts., Deep Canyon, *Roos 3427* (RSA). San Bernardino Co., New York Mts., Keystone Canyon (cultivated from *Wolf 9532*), *Balls 9152* (BM), *10235* (MB, E), *18923* (RSA, TEX), *19775* (RSA, TEX); 11 mi. S of Cima, *Gregory 374* (RSA, UC); W slope of Providence Mts., Columbia Mine, *Wolf 10715* (RSA, TEX, US). Tuolomne Co., Piute Creek, 1893, *Wilson s.n.* (UC). COLORADO: Archuleta Co., 15 mi. N of Arboles, *Harrington 4121* (CS). Eagle Co., Wolcott, Eagle River, *Pennell & Schaeffer 22260* (PH). Garfield Co., Glenwood Springs, *Osterhout 2595* (NY, RM, WIS). Gunnison Co., Black Canyon of the Gunnison, *Dunn 15251* (UMO). Moffat Co., 8.7 mi. E of Craig along Hwy. 40, *Wagner 4048* (MO). Montezuma Co., 2 mi. SW of Dolores, *Harrington 10121A* (CS). Montrose Co., Black Canyon Nat'l. Monument, East Portal, *Weber & Miller 11385* (COLO, DAO). Pitkin Co., above Snowmass, Trappist Monastery, *Rambolt 47* (DS). Rio Blanco Co., E of Meeker, *Harrington 4544* (ARIZ, CS). Routt Co., 11.6 mi. W of jct. rd. to Clark and Hwy. 40, *Wagner 4047* (MO); Elk River Valley, 6.4 mi. N jct. Hwy. 40 and County Rd. 129, *Wagner 4046* (MO); between Clark and Seedhouse G.S., *Weber 6945* (CAS, COLO, DAO, MIN, RSA, WS). San Miguel Co., 1 mi. W of Sawpit, Hwy. 145, *Stockhouse 173* (MO). IDAHO: Ada Co., Boise, *Clark 42* (BH, CAN, DS, E, F, G, GH, MIN, MO, NY, PH, POM, RM, UC). Bannock Co., 1.8 mi. W of Franklin Co. line, Hwy. 191, *Stockhouse 553* (MO). Bear Lake Co., Montpelier, *Macbride 1* (BRY, CS, DS, E, F, G, MIN, MO, NY, RM, UC, WS). Blain Co., Picabo, *Macbride & Payson 2988* (CAS, DS, E, GH, MO, NY, POM, RM, UC). Bonneville Co. (T1N, R44E), *Holte 7* (WS). Butte Co., W of Big Lost River Bridge on Hwy. 20/26, *Atwood 880* (BRY, NY, WTS). Cassia Co., Raft River Valley, 1929, *Biggers s.n.* (IDS, NY). Clark Co., 9 mi. SW of Dubois, Hwy. 22, *Hitchcock & Muhlick 22782* (DAO, NY, WS). Franklin Co., Cub River, 8 mi. E of Preston, *Bright 60230* (MIN). Fremont Co., 4.8 mi. E and 2.5 mi. N of St. Anthony, *Raven & Gregory 19558* (ARIZ, BM, DAO, DS, G, OSC, RSA, US); lava outcrops on dunes, 5 mi. W of St. Anthony, *Stockhouse 238* (MO). Gem Co., Emmett, *Macbride 778* (ASC, BH, CAN, DS, E, F, G, GH, ID, MIN, MO, NY, POM, RM, UC, UTC, WS). Idaho Co., Snake River Canyon above mouth of Sheep Creek, *Constance et al. 1603* (ND, POM). Lincoln Co., 9 mi. N of Richfield, *Christ 51-117* (ID). Madison Co., W of Rexburg, *Cronquist & Davis 2074* (MO). Nez Perce Co., Lewiston, *Heller & Heller 32113* (CU, DAO, DS, E, G, MIN, MO, NY, PH, UC, WS). Oneida Co., 9 mi. W of Malad City, on Rt. 37, Blue Spring Hills, *Holmgren & Jensen 3469* (ARIZ, ASU, BRY, CAS, ID, NY, UMO, UNLV, US, UT, UTC, WTS). Owyhee Co., Murphy, *Macbride 1031* (ASC, BH, CAN, DS, E, F, G, GH, MIN, MO, NY, POM, RM, WS). Washington Co., 5 mi. N of Rebecca, *Christ 9350* (NY). NEVADA: Carson City, Carson City, *Anderson 74* (GH, US). Churchill Co., 3 mi. W of Boyer Ranch, Dixie Valley, *Tiehm & Birdsey 4894* (MO). Clark Co., SW slope of Spring Mts., *Beatley & Reveal 10811* (NTS, RSA); Charleston Mts., Lee Canyon, *Clokey 8040* (ARIZ, BH, BRY, CAN, COLO, CS, CU, DAO, DS, F, G, GH, LA, MICH, MIN, MO, MONTU, NA, ND, NDA, NO, NY, OSC, PH, RENO, RM, RSA, SD, TEX, UC, UMO, US, UT, UTC, WIS); Charleston Mts., Kyle Canyon, *Gregory 383–86, 388* (RSA); Charleston Mts., Charleston Park, *Gregory 439* (CAS, RSA, UC). Elko Co., Ruby Mts., above Cave Creek P.O., *Heller 9509* (E, NESH, NY, PH). Esmeralda Co., Palmetto Range, *Purpus 5882* (E, UC). Eureka Co., Palisade, *Raven 15416* (RSA, UC). Lander Co., Kingston Canyon, 2 mi. below Ranger Station, *Goodner & Henning 206* (NA, POM, RENO). Lincoln Co., Meadow Valley Wash, 5 mi. SE of Elgin, 21 mi. S of Caliente, *Holmgren & Holmgren 7814* (BRY, NY, UTC). Lyon Co., 2 mi. W of Silver City, American Flat Canyon, *Allen 105* (NA, POM, UC). Mineral Co., SW base of Mt. Grant, *Heller 10904* (DS, E, F, G, GH, MO, NY, PH, UC). Nye Co., Stonewall Mt., *Alexander &*

Kellogg 2463 (POM, UC); Shoshone Mt., SW of Tonopah Spring, *Beatley 5639* (DS, RENO, RSA, UTC); Central Rainier Mesa, Yucca Flats area, *Beatley 3873* (DS, RENO, UNLV); Belted Range, below Cliff Spring, *Beatley & Kaaz 8881* (NTS, DS, RSA); Hot Creek Range, 1 mi. NE Marcy Peak, *Klein 2612* (MO); 2 mi. S of March Peak, *Klein 2642* (MO). Pershing Co., Rochester, 1933, *Train s.n.* (ARIZ, YU). Storey Co., SE of Virginia City, Six Mile Canyon, *Allen 165* (MO, NA, POM, RENO). Washoe Co., Virginia Mts., Truckee Pass, *Kennedy 1332* (ARIZ, CU, DS, MO, NESH, NMC, NY, UC). White Pine Co., Egan Range, 0.5 mi. W of Ely on Hwy. 50, *Tiehm et al. 5305* (BRY, MO). NEW MEXICO: Bernalillo Co., Albuquerque, West Mesa, *Krammerer 13* (NY, TEX). Catron Co., Bat Cave, San Augustin Plains, *Smith 150* (ARIZ, DAO, PH). Dona Anna Co., San Andres Mts., Five-Rams Spring, *Sandoval 64, 65* (UNM). Grant Co., Burro Mts., *Metcalfe 200* (ARIZ, BM, E, G, GH, MIN, MO, NESH, NMC, NY, POM, RM, UC). Hidalgo Co., San Luis Pass, 1937, *collector unknown s.n.* (NMC). Lincoln Co., White Mts., South Fork of Tularosa Creek, 1897, *Wooton s.n.* (G, MIN, MO, NY). McKinley Co., Bluewater Lake, *Mollica 27* (MO). Rio Arriba Co., Santa Barbara Canyon, *Thurber 290* (GH, NY). Sandoval Co., 31 mi. SW of Santa Fe, Hwy. 85, *Klein 1479* (RSA, UC); 2 mi. S of Bernalillo along I-25, *Wagner et al. 4401* (MO). Santa Fe Co., Santa Fe Canyon, *Heller & Heller 3773* (BH, BM, CU, E, G, MIN, NY). San Juan Co., Chuska Mts., Washington Pass, 1955, *Clark s.n.* (UNM). Sierra Co., 11 mi. W of Cuchillo, Hwy. 52, *Martin 4822* (UNM). Socorro Co., Magdalena Mts., Water Canyon, *Herrick & Herrick 54* (F, NY); Taos Co., Rio Grande Gorge, *Spellenberg & Spellenberg 4971* (MO). Valencia Co., Zuni Mts., La Jara Spring, *Riffle 1122* (UNM). OREGON: Baker Co., 1.5 mi. NE of Huntington, Burnt River, *Hitchcock & Muhlick 20999* (DAO, DS, NY, WS). Harney Co., Steins Mt., 1935, *Train s.n.* (DAO, MIN, OSC, UMO). Malheur Co., 25 mi. SW of Vale, *Hitchcock 20673* (CAN, NY, WS). Wallowa Co., Imnaha River, Thorn Creek Gard. Sta. *Kruckeberg 2329* (CAN, COLO, DAO, GH, ID, NY, RM, RSA, UC, UTC, WS). Wheeler Co., John Day Valley, Muddy Station, 1885, *Howell s.n.* (G, OSC). Without county, E Oregon, Snake River, *Cusick 2542* (CU, E, GH, MIN, NY, WS). UTAH: Beaver Co., WahWah Mts., Pine Canyon, *Maguire 20926* (BRY, DAO, GH, NY, UC, UTC). Box Elder Co., Wellsville Mts., Two Jump Canyon, 0.5 mi. NE of Relay Station, *Wagner 4065* (MO). Cache Co., Wellsville Range, Pine Canyon, *Maguire 3045* (MO, POM, UC, UTC). Daggett Co., Eastern Uinta Mts., Sheep Creek Canyon, *Porter & Rollins 5656* (DAO, DS, GH, RM, UC). Davis Co., Antelope Island, *Watson 411* (GH, NY). Duchesne Co., 15 mi. SW of Myton, Wells Draw, *Brotherson 758* (BRY, UMO). Emery Co., Wasatch Mts., Hwy. 29 along Seely Creek, *Pennell et al. 22724* (PH). Garfield Co., Dixie Nat'l. Forest, Aquarius Plateau, Cowpuncher Creek, *Maguire 17178* (BRY, DAO, NY, UTC). Grand Co., Book Mt., 20 mi. NE of Thompson, *Foster & Foster 4999* (BRY, WTS). Juab Co., 7.2 mi. N of Mona, *Pitts 4* (UT, UTC). Kane Co., near Glendale, Hidden Lake, *Jones 25275* (BM, DS, MICH, MO, MONTU, ND, POM, RSA, UCLA). Millard Co., Dome Canyon, Horse Range, *Peabody et al. 382* (BRY, MO, NY, UMO, WTS). Piute Co., Marysvale, *Jones 5375* (BM, G, NY, POM, RM, UC, US). Salt Lake Co., Salt Lake City, *Jones 1746* (DS, F, GH, MICH, MIN, NY, POM, RM, UTC); Sandy, 1884, *Leonard s.n.* (GH). San Juan Co., 40 mi. SE of Hite Natural Bridges, White Canyon, *Harrison 11604* (BRY, RSA). Sevier Co., Glenwood, *Ward 16* (MO). Tooele Co., Stansbury Range, S Willow Creek Canyon, *Maguire 21822* (DAO, GH, RSA, UC, UTC, WS). Uintah Co., 25 mi. NE Vernal, Warren Draw, *Neese 5698* (BRY). Utah Co., Diamond Valley, *Goodding 840* (CU, G, GH, MO, NY, RM). Wasatch Co., near Midway, Snake Creek, *Harris 27338* (MIN, PH). Washington Co., between Zion Junction and Zion Nat'l. Park, *Nelson & Nelson 2687* (GH, MO, NY, RM, UC, US). Wayne Co., Thousand Lake Mt., *Dixon 442* (F). Weber Co., Ogden, *Shoop 50* (F, UMO). TEXAS: Culberson Co., McKittrick Canyon, Guadalupe Mts., *Moore & Steyermark 3788* (MO); Pine Top Mt., *Turner & Warnock 181* (GH). WASHINGTON: Asotin Co., 4 mi. S of Clarkston, *St. John & Brown 3905* (DS, MO, NY, RM, UC, WS). Whitman Co., Wilma, *St. John & Warren 3402* (MO, NY, UC, WS). WYOMING: Lincoln Co., 7.5 mi. W of Opal, Hwy. 30N, *Stockhouse 127* (MO); 5.3 mi. E of jct. Hwy. 190 on 30N, *Wagner 4057a* (MO); Hwy. 30, 3.3 mi. E of Hwy. 189 jct., *Wagner 4054-B* (MO). Uinta Co., 3 mi. SW of Evanston, *Goodman 4492* (NY, RM).

Intermediate between *Oenothera caespitosa* subsp. *marginata* and subsp. *navajoensis*:

ARIZONA: Coconino Co., near Tuba City, *Peebles & Fulton 11854* (ARIZ, US); Painted Desert, N of Cameron, *McKelvey 4470* (GH). COLORADO: Eagle Co., roadcut 4 mi. SE of Wolcott, *Klein 1108–1110* (RM, RSA, UC). UTAH: Carbon Co., left-fork of Minnie Maud Creek, West Tavaputs Plateau, 20 mi. N of Wellington, *Maguire 18541* (NY, UTC). Duchesne Co., Wells Draw, 15 mi. SW of Myrton, *Brotherson 758* (MO), *1079* (BRY). Emery Co., Horn Mts., Rock Canyon near Daniels Canyon, *Allen 711* (UT); San Rafael Swell, Canyon of San Rafael Reef, *Harris 98* (BRY). Kane Co., 8 mi. E of Kanab, roadside, *Foster 3762* (BRY); 5.5 mi. below Klondike Bar, Glen Canyon, *Gaines 933* (ASC, MNA). Sanpete Co., San Pitch Mts., Wales Canyon, *Collins & Harper 48* (BRY). Sevier Co., Fish Creek Canyon, *Garrett 2506* (NY).

Intermediate between *Oenothera caespitosa* subsp. *marginata* and subsp. *caespitosa*:

IDAHO: Bannock Co., Pocatello, *Soth P-70* (RM). UTAH: Box Elder Co., near Honeyville, Wellsville Mts., Two Jump Canyon, horse corral (one plant), *Wagner 4064* (MO); sagebrush slope (mixed with subsp. *marginata*), *Wagner 4065* (MO). Cache Co., Paradise, 1935, *Lee s.n.* (WIS); Providence, near Smith Arboretum, *Maguire 3603* (CU, UTC); near Midway, Hot Pot, *Keck 716* (DS, POM).

Intermediate between *Oenothera caespitosa* subsp. *marginata* and subsp. *crinita*:

ARIZONA: Mojave Co., Kingman, *Eastwood 18020*, pro parte (CAS). CALIFORNIA: Inyo Co., Squaw Flat road, E of Blue Bell Mine, *Roos & Roos 5993* (DS, RSA). Mono Co., White Mts., Cottonwood Creek, *Duran 1648* (UC). Without County, Barnwell, 1911, *K. Brandegee s.n.*, pro parte (UC). NEVADA: Clark Co., Charleston Mts., Kyle Canyon, *Gregory 387* (RSA); Charleston Mts., Indian Spring, 1906, *Jones s.n.* (POM).

Specimens of Arizona race with short floral tubes:

ARIZONA: Coconino Co., Grand Canyon, South Rim, Yavapai Point, *Comstock 711* (ARIZ), Sunset Crater Nat'l. Monument, Bonito Lava Flow, *Eggler 809* (MNA); Wupatki Nat'l. Monument, 1939, *Jones s.n.* (ARIZ); high tension line from Leupp Hwy. to Sunset Crater, *Mason et al. 2628* (ARIZ); Sunset Crater Nat'l. Monument, 1956, *McDougall s.n.* (MNA); 18 mi. NE of Flagstaff, *Munz 13034* (CU, POM, UC); San Francisco Mts., *Purpus 7082* (US); Jack Smith's Tank, 1935, *Whiting s.n.* (MNA); San Francisco Mts., Summit Ranch, *Thornber 2852* (ARIZ). Yavapai Co., 3 mi. NW of Prescott, *Glowenke 10912* (PH); Mingus Mt., near Jerome, 1967, *E. Jones s.n.* (ASU, OSC); Skull Valley, 1903, *M. Jones s.n.* (POM); S of Seligman on rd. to Prescott, *McKelvey 4082* (GH); 1 mi. S of Humboldt, *Newlon 764* (JEPS); E of Ft. Whipple, Prescott, *Tidestrom 12729* (NA); ¼ mi. S of Prescott, *Tolonen 20-N* (BM); 1 mi. S of Humboldt, *Wiegand & Upton 3903* (CU).

Oenothera caespitosa subsp. *marginata* is the most common and widespread of the taxa in the *O. caespitosa* group, and is the only subspecies that intergrades with all of the other four subspecies. This entity is quite distinctive with its large (usually over 16 cm) pinnately lobed to coarsely dentate leaves; stiffly erect, usually dense pubescence; large flowers with floral tubes mostly 8–16 cm long; and symmetrical, cylindrical capsules, these often on a long pedicel (1–6 cm).

As delimited here, *Oenothera caespitosa* subsp. *marginata* is similar to the concept of Munz (1931b, 1965), with a few discordant populations included by Munz placed in *Oenothera caespitosa* subspp. *crinita* or *navajoensis*. One such group consists of plants from low and middle elevations in Nevada and in the Inyo region in California with floral tubes 4–7.5 cm long, leaves 5–17 cm long, capsules asymmetrical at the base, ribbed seed-collars, and flowers that fade rose purple to rose. In the present treatment, they are included under subsp. *crinita*. Their capsule and seed characters clearly show the close relationship between them and the small-flowered, pulvinate plants of high elevations or unusual edaphic sites at lower elevations that comprised subsp. *crinita* in the sense of Munz. Since seed and capsule features are not commonly seen on specimens, Munz gave more weight to the larger pinnately-lobed leaves of these plants which are generally more similar to those of subsp. *marginata* than they are to the smaller (2–7 cm), often nearly entire leaves of the pulvinate form of subsp. *crinita*. When much more material than Munz had available was examined, it became quite clear that the leaves of the pulvinate form are just an extremely reduced and more densely pubescent form of the larger leaves of subspp. *crinita* and *marginata*, and they grade rather smoothly from one extreme to the other. Likewise, several collections consisting of robust caulescent individuals of *Oenothera caespitosa* subsp. *navajoensis* were annotated by Munz as subsp. *marginata*, although these plants had shorter floral tubes and capsules different from those found in subsp. *marginata*

Oenothera caespitosa subsp. *marginata* exhibits a very complex pattern of variation. A considerable portion of this variation occurs within individual populations and may in part represent phenetic variability without a genetic basis. This kind of variation primarily involves size and density differences in various parts, especially of the leaves, stems, capsules, and floral tubes. Some variation consists of weakly marked trends of concordant characters or sometimes discordant single characters; although probably genetic, it does not define units that can appropriately be recognized taxonomically. A second source of variability is hybridization between *O. caespitosa* subsp. *marginata* and the other subspecies, which has sometimes been followed by the stabilization and subsequent spread of the derivative populations.

Robust plants with stems up to 4 dm occur sporadically nearly throughout the range of *Oenothera caespitosa* subsp. *marginata*; they predominate, however, only in Arizona from along the Mogollon Rim to the margins of the Sonoran Desert, the Inyo region of southern California, and the High Plateau regions of southwestern to south-central Utah. These plants also have extremely long leaves, up to 30–36 cm long, and the longest pedicels in the subspecies (to 5.5 cm long), the longest of which was recorded from plants from Piute County, Utah [e.g., near Marysvale, *Grant & Grant 9686* (RSA, UC)]. Plants that are acaulescent or have several to many short stems predominate elsewhere, particularly at higher elevations, but they also occur in the same geographical area as the long-stemmed plants and sometimes in the same population. Asa Gray described *O. eximia* from one of the robust, long-stemmed plants from Santa Fe, New Mexico, but the epithet had subsequently been misapplied to the strictly caulescent *O. harringtonii* from southeastern Colorado.

The distribution of plants in which the leaves and buds have reddish purple splotches, a primitive character for the *O. caespitosa* group, roughly parallels that of the caulescent plants, ranging

TABLE 13. Comparison of floral tube lengths between different populations of *Oenothera caespitosa* subsp. *marginata*.

Locality and Voucher (Ranked by Magnitude of Means)	Population Mean (cm)	Number of Individuals Measured	Variance (cm^2)
1. Grant Co., NM, *Metcalfe 200*	13.9	10	4.2709
2. Coconino Co., AZ, *Gregory 435*	12.3	7	0.6155
3. Nye Co., NV, *Beatley & Kaaz 8881*	11.9	3	0.7267
4. San Bernardino Co., CA, *Wolf 10715*	11.8	8	1.8893
5. Santa Cruz Co., AZ, *Peebles & Fulton 11448*	11.7	6	2.0667
6. Pinal Co., AZ, *Lehto, Hensel & Pinkava 11000 A + B*	11.3	6	0.4980
7. Kane Co., UT, *Jones 25275*	11.0	13	0.6315
8. Santa Cruz Co., AZ, *Holmgren & Holmgren 6831*	10.8	5	1.0216
9. Inyo Co., CA, *Duran 552*	10.5	17	1.8865
10. Washoe Co., NV, *Kennedy 1332*	10.2	6	1.1967
11. Clark Co., NV, *Beatley & Reveal 10811*	9.6	6	1.756
12. Piute Co., UT, *Jones 5375*	9.4	12	0.5983
13. Daggett Co., UT, *Porter & Rollins 5656*	8.7	6	0.3714
14. Salt Lake Co., UT, *Jones 1746*	7.5	19	0.8127
15. Ada Co., ID, *Clark 42*	7.2	10	0.9849
16. Bear Lake Co., ID, *Macbride 1*	7.1	12	0.7208
17. Baker Co., OR, *Hitchcock & Muhlick 20999*	6.9	4	0.0669
18. Baker or Mahlhuer Co., Snake River, E OR, *Cusick 2542*	6.7	18	0.5710

from central to western Arizona, California (particularly San Bernardino County), and northward through central Utah to Idaho. Plants without splotches on the leaves also occur throughout this same region.

Very striking plants completely lacking long erect hairs or with only a few of them but retaining the dense covering of minute glandular hairs are known from Inyo County, California, and from scattered localities in southern Nevada. These were described by A. A. Heller as *Anogra longiflora* and recognized as *O. caespitosa* var. *longiflora* by Munz (1931b). In 1965 Munz reduced this entity to synonymy under subsp. *marginata*. Although plants of this sort often occur in pure populations, they do not seem to differ ecologically from hirsute plants of the same general area. Moreover, plants of the two sorts sometimes occur intermixed (e.g., the type collection; Westgard Pass, Inyo Co., California, *Eastwood & Howell 9604*), and therefore do not seem to merit formal recognition.

Two collections from the Pyramid-Winnemucca Lake region, *Kennedy 2049* (DS) and *K. Brandegee 2049K* (UC) and one from 5 mi. south of Sutcliffe, Washoe County, Nevada, *Pinzl 11* (RENO), are similar in their complete or near lack of hirsute hairs, but are atypical in their narrow forward-pointing leaf lobes and 7–8.5 cm long floral tubes. They are included here because of their obvious similarities to subsp. *marginata* especially in their seeds, but the short floral tubes suggest possible hybridization with subsp. *crinita*, which also occurs in the area.

Another interesting series of populations is from south-central Arizona, from Gila County south to Santa Cruz County then northwest along the margin of the Sonoran Desert to Yavapai County, in which the seed-collars are greatly inflated, the embryo portion constituting only 15–25% of the total seed volume (Figs. 48–50, 85), and the seeds are often arranged in one irregular row or two overlapping ones. Otherwise the plants do not differ greatly from many other populations of subsp. *marginata*.

There is considerable variation in the length of the floral tube in *Oenothera caespitosa* subsp. *marginata*, but less than in *O. caespitosa* subsp. *macroglottis*. In *O. caespitosa* subsp. *marginata*, there is a noticeable reduction in the size of the floral tubes from south to north. Population means and variances of 18 populations (based on multi-individual collections in herbaria) from throughout the range of subsp. *marginata* were measured (one flower per individual; Table 13). In order to compare each mean to every other,

TABLE 14. Paired comparisons among population means of floral tube lengths of *Oenothera caespitosa* subsp. *marginata* (Student-Newman-Keuls test). Differences without an asterisk (*) or plus (+) were not tested because a larger range was found to be not significant.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		13.9	12.3	11.9	11.8	11.7	11.3	11.0	10.8	10.5	10.2	9.6	9.4	8.7	7.5	7.2	7.1	6.9	6.7
1	13.9																		
2	12.3	1.6*																	
3	11.9	2.0*	0.4																
4	11.8	2.1*	0.5	0.1															
5	11.7	2.2*	0.6	0.2	0.1														
6	11.3	2.6*	1.0	0.6	0.5	0.4													
7	11.0	2.9*	1.3	0.9	0.8	0.7	0.3												
8	10.8	3.1*	1.5	1.1	1.0	0.9	0.5	0.2											
9	10.5	3.4*	1.8	1.4	1.3	1.2	0.8	0.5	0.2										
10	10.2	3.7*	2.1+	1.7	1.6	1.5	1.1	0.8	0.6	0.3									
11	9.6	4.3*	2.7*	2.3+	2.2	2.1	1.7	1.4	1.2	0.9	0.6								
12	9.4	4.5*	2.9*	2.5*	2.4*	2.3*	1.9*	1.6*	1.4+	1.1	0.8	0.2							
13	8.7	5.2*	3.6*	3.2*	3.1*	3.0*	2.6*	2.3*	2.1*	1.8*	1.5+	0.9	0.7						
14	7.5	6.4*	4.8*	4.4*	4.3*	4.2*	3.8*	3.5*	3.3*	3.0*	2.7*	2.1*	1.9*	1.2*					
15	7.2	6.7*	5.1*	4.7*	4.6*	4.5*	4.1*	3.8*	3.6*	3.3*	3.0*	2.4*	2.2*	1.5*	0.3				
16	7.1	6.8*	5.2*	4.8*	4.7*	4.6*	4.2*	3.9*	3.7*	3.4*	3.1*	2.5*	2.3*	1.6*	0.4	0.1			
17	6.9	7.0*	5.4*	5.0*	4.9*	4.8*	4.4*	4.1*	3.9*	3.6*	3.3*	2.7*	2.5*	1.8*	0.6	0.3	0.2		
18	6.7	7.2*	5.6*	5.2*	5.1*	5.0*	4.6*	4.3*	4.1*	3.8*	3.5*	2.9*	2.7*	2.0*	0.8+	0.5	0.4	0.2	

* Significant at $P = 0.05$.
+ Not significant at $P = 0.05$.

a Student-Newman-Keuls test was performed on this data (Table 14). The results of the analysis can be summarized by bracketing those ranges of population means which were found to be not significantly different (Table 14).

Several points can be derived from this analysis:

1. Population 1, which is representative of populations from the southeastern portion of the Mogollon Rim in Arizona to the mountains of southwestern New Mexico, was significantly different from all others. We have not made observations of the pollination spectrum in this area, but as pointed out by Gregory (1964), the potential hawkmoth pollinators with tongues up to 14 cm such as *Manduca rustica* (Fabricius), *Agrius cingulatus* (Fabricius), and *Cocytius antaeus* (Drury) occur in this area. It is interesting to note that almost all of the other montane species of *Oenothera*—*O. flava* (sect. *Lavauxia*), *O. brachycarpa* (sect. *Megapterium*), *O. organensis* (sect. *Oenothera*) and *O. muelleri* (sect. nov. in prep.)—from this area, the adjacent isolated mountains of southern New Mexico and the mountainous regions of northern Mexico, all have floral tubes well over 12 cm long. The evolution of long tubes in *O. caespitosa* and each of the other sections evidently represents parallel evolution.

2. There is a cline of decreasing floral tube lengths from south to north that links populations 2 through 13 and includes most of the geographical and ecological range of subsp. *marginata*.

3. Populations 14 through 18 are sharply distinct from 1 to 13. This pattern is almost certainly related to very low densities or lack of long-tongued hawkmoths in Idaho, Oregon, and Washington. There is also a parallel overall reduction from south to north in the size of other plant parts. In general plants of *Oenothera caespitosa* subsp. *marginata* from New Mexico to California, Nevada, and Utah typically have leaves 17–35 cm long, floral tubes 8.5–15 cm long, and petals 4–6 cm long, whereas the Idaho, Oregon, and Washington plants are modally different with leaves 6–15 cm long, floral tubes 5–9 cm long, and petals mostly 3–4.5 cm long.

4. Population 14 deserves special mention because a second factor contributes to its shorter floral tubes and leaves. There is some degree of intergradation between *Oenothera caespitosa* subspp. *crinita* and *marginata* in the vicinity of the Great Salt Lake that may have contributed to the shorter floral-tube lengths of populations from this area. If population 14 is removed from consideration, the steepness of the cline between populations 13 and 15 is even more striking. It seems unlikely that additional sampling would link populations 2 through 14 to 15 through 18.

2. Oenothera psammophila (A. Nels. & Macbr.) W. L. Wagner, Stockhouse & Klein, comb. nov. *Pachylophus psammophila* A. Nels. & Macbr., Bot. Gaz. (Crawfordsville) 61: 32. 1916. TYPE: Sand Hills, 10 mi. W of St. Anthony, Fremont Co., Idaho, 8 July 1901, *Merrill & Wilcox 888* (lectotype here designated, RM-32393, photo MO; isolectotypes, GH, NY, US not seen). This is the only known collection made prior to 1916, when Nelson and Macbride described this species. Moreover, it is the only collection of *Oenothera psammophila* at RM, where Aven Nelson was employed at the time this entity was described. *Oenothera caespitosa* Nutt. var. *psammophila* (A. Nels. & Macbr.) Munz, Amer. J. Bot. 18: 733. 1931. Davis, Fl. Id. 497. 1952. Hitchcock et al., Vasc. Pl. Pac. Northw. 495. 1961. Hitchcock & Cronquist, Fl. Pac. Northw. 310. 1973. Figure 110.

Loosely caespitose perennial herb forming clumps 3–6 dm across from a woody taproot; primary stem, 1–3 dm long, decumbent, but soon becoming woody and buried in sand, the numerous secondary branches arising from leaf axils of primary stem, reddish to straw-colored, glabrous. Leaves green, lustrous, thick and leathery, glabrous with resinous exudate especially on the younger leaves causing sand particles to adhere (sand sheath), narrowly oblanceolate to oblanceolate (6–)8–9(–14.2) cm long, (0.7–)1.5–2(–3.1) cm wide, the apex acute usually a minute callous tip, the margins subentire to repand or remotely dentate, rarely serrate, the teeth 0.5–2.5 mm high, gradually tapering to a winged petiole 3–9 cm long. Buds erect without free sepaltips, ca. 1 cm diam., resinous when young. Flowers with a sweet scent, 1–3 per stem opening per day near sunset, floral platform usually not horizontal, often nearly vertical. Ovary covered with a thick resinous exudate, 16–28 mm long, sessile. Floral tube 4.2–6 cm long, 1.6–1.8 mm diam. medially, flaring to 7–10 mm at the mouth, glabrous. Sepals yellowish green, the veins lightly infused with reddish purple pigment, narrowly

FIGURE 110. *Oenothera psammophila*; Fremont Co., Idaho, isolectotype, *Merrill & Wilcox 888* (NY).

lanceolate, acute at the apex, 22–28 mm long, 4–6 mm wide, glabrous. Petals fading rose pink to rose, glabrous, 2.3–4 cm long, 2.7–4.8 cm wide, the notch 3–5 mm deep. Staminal filaments 17–19 mm long; anthers 13–16 mm long. Style 6–7.2(–8.8) cm long, well elevated above or outside the ring of stamens; stigma lobes 3.5–6 mm long. Capsules (1–)3–4(–10) maturing per stem, lance-cylindrical, nearly terete, somewhat curved, symmetrical at the base, cuneate, (2–)3–4.7 cm long, 7–8 mm diam., gradually tapering to a sterile portion 6–8 mm long, the free tips 1.5–2 mm long, erect or slightly recurved sometimes somewhat twisted, the margins of the valves with a conspicuous irregularly wavy ridge, 1–2.5 mm high, dehiscing nearly throughout the length of the capsule, pedicel 1–5 mm long. Seeds 50–90 per capsule in two distinct rows, the raphe parallel to the plane of the capsular axis, narrowly obovoid usually curved, light to very dark reddish brown, 2.5–3 mm long, 1.2–1.4 mm wide, 0.9–1 mm high; embryo portion constituting ca. ⅞ of the seed volume, finely reticulate; seed-collar with a broad membrane sealing the cavity, the margin entire, the surface finely pustulate-reticulate. Self-incompatible. Gametic chromosome number, $n = 7$.

Distribution (Fig. 111). On barren areas of drifting sand at the interface between outcrops

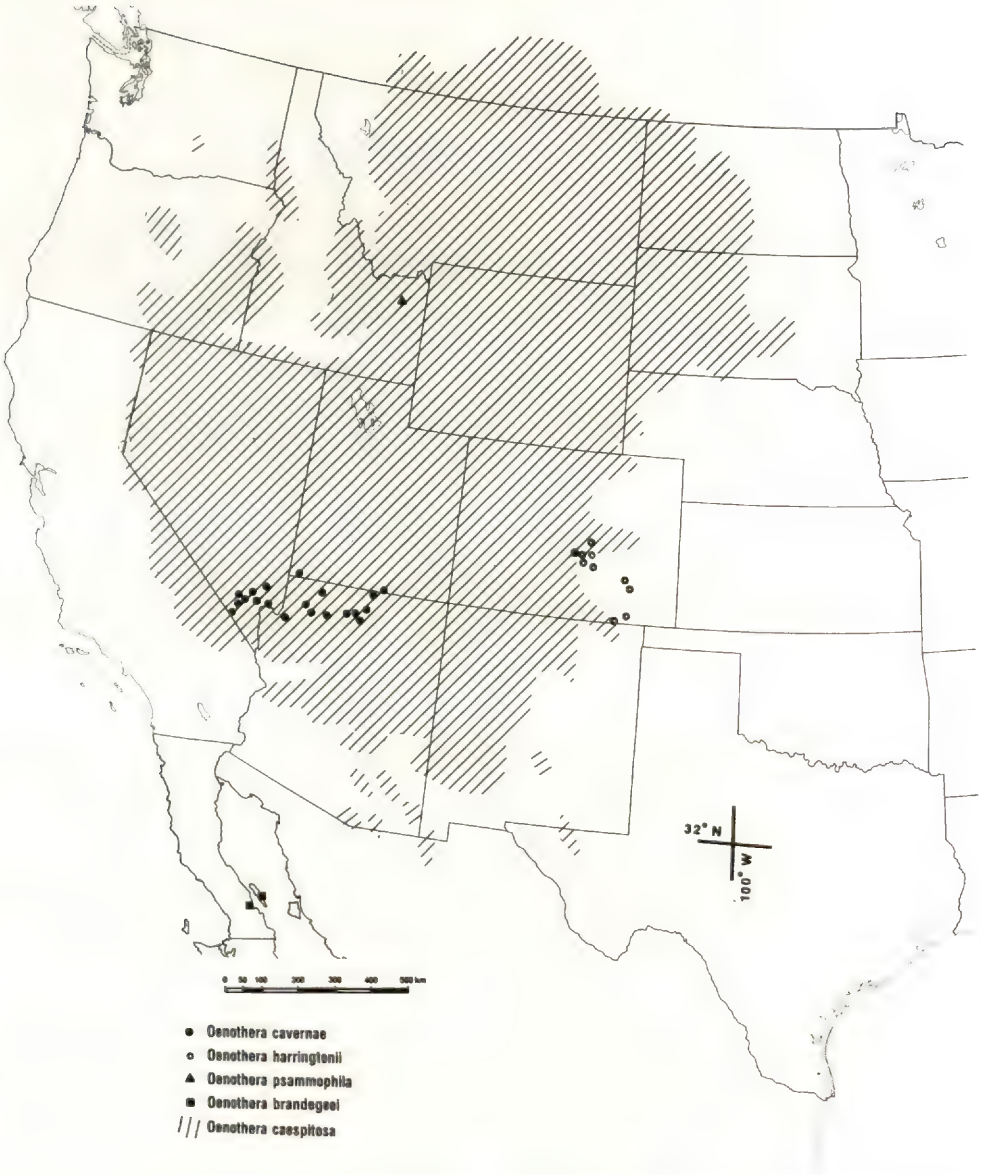


FIGURE 111. Distributions of *Oenothera psammophila, O. harringtonii, O. cavernae,* and *O. brandegeei.*

of lava and sand dunes, only known from the dune area north and west of St. Anthony, Fremont County, Idaho, 1,500–1,650 m. Flowering from May to early July.

Additional specimens examined. UNITED STATES. IDAHO: Fremont Co., Egin, near St. Anthony, *Quayle 29* (DS, NY, RM, UC); 1.3 mi. N of Egin, *Raven & Gregory 19568* (ARIZ, BM, DAO, DS, G, GH, MICH, NY, OS, RM, SD, UC); St. Anthony Sand Dunes, 1 mi. N of Parker, *Stockhouse 247* (MO); 3.8 mi. W and 1.3 mi. N of Parker Jct., *Wagner 4061* (MO).

Oenothera psammophila is the most specialized perennial in the *O. caespitosa* group. The long decumbent stems, which become buried in drifting sand, coupled with the profusion of secondary branches arising in the leaf axils of the

primary stem and the heavy vicid exudate to which sand adheres all appear to be adaptations to the dune habitat. The function of other specialized features, such as the vestigial seed-collar, lack of pubescence, and the somewhat twisted capsules, are not understood.

The only known locality of this dune specialist is within the ranges of its presumed progenitors *Oenothera caespitosa* subspp. *caespitosa* and *marginata*. A comprehensive survey of the dunes by Stockhouse (1973) revealed no intermediates. Plants of subsp. *marginata* grow on stable flats and rock outcrops in and near dunes, while *O. psammophila* grows only in lava where there is shallow drifting sand. The sharp difference between their habitats undoubtedly is the greatest barrier to hybridization. Some of the experimental hybrids between *O. psammophila* and *O. caespitosa* subsp. *marginata* were pale green or yellowish, which suggests a greater degree of genetic differentiation between these entities than between the subspecies of *O. caespitosa*. This result suggests plastid or genomic differentiation between *O. psammophila* and *O. caespitosa* subsp. *marginata*. Even if hybridization occurred in nature, the probability of establishment of the hybrid individuals should be very low. In addition, they are modally pollinated by different moths. Noctuid moths and rarely *Hyles lineata* and *H. gallii* are the principal pollinators of *Oenothera psammophila* while species of *Sphinx, Manduca,* and *Hyles* pollinated *O. caespitosa* subsp. *marginata* at the dunes (Stockhouse, 1973). Thus both external and internal barriers operate in the separation of *O. psammophila* from *O. caespitosa* subsp. *marginata*.

Oenothera psammophila has been proposed in the list of potentially threatened and endangered plant species of the United States (U.S. Fish and Wildlife Service, 1980: 82524) as an endangered species. The critical habitat for this species is a broken belt of sand dunes ca. 2–3 km wide extending from northeast to southwest for about 32 km. The habitat of *O. psammophila* is very specific; plants grow only in areas of shallow, relatively stable sand underlain by lava. Thus the actual area available for *O. psammophila* to grow is considerably smaller than the total dune area. *Oenothera psammophila* is restricted to the periphery of the dunes and to blowout areas that are scattered throughout the dunes. Stockhouse surveyed roughly one-third of the total dune area in 1972. Populations were scattered throughout the area surveyed. Most sites that appeared to fit the requirements for *O. psammophila* supported healthy populations, generally containing 200–500 individuals. Because populations are scattered about and no specific attempt was made to census *O. psammophila,* it would be very difficult to make an accurate estimate of the number of individuals of *O. psammophila* in existence. A conservative estimate would certainly be over 10,000 individuals.

Potential threats to *Oenothera psammophila* are grazing or trampling by cattle (the land is managed by the Bureau of Land Management) or damage by motorized dune vehicles. Neither Stockhouse in 1972 nor Wagner in 1979 noted any damage by either potential source. Although dune vehicles are common in the area they travel in deep sand and not over the rocky sites inhabited by *O. psammophila*. Thus at the present time there are no apparent threats to this species' continued existence so long as the habitat is maintained in its current state and the pollinators continue to survive.

3. **Oenothera harringtonii** W. L. Wagner, Stockhouse & Klein in Wagner, Ann. Missouri Bot. Gard. 70: 195. 1983. TYPE: Colorado Springs, El Paso Co., Colorado, 2,000 m, 29 May 1939, *Ehlers 7461* (holotype, MICH, photos MO, COLO; isotypes, MICH 2 sheets, NA). Figure 112.

Pachylophus exiguus sensu Rydb., Bull. Torrey Bot. Club 30: 260. 1903, pro parte (as to plants from Colorado), non (A. Gray) Woot. & Standl. *Pachylophus eximius* sensu Woot. & Standl., Contr. U.S. Natl. Herb. 16: 157. 1913, pro parte (as to plants from Colorado), non (A. Gray) Woot. & Standl. Rydb., Fl. Rocky Mts. 598. 1922, pro parte; Fl. Plains N. Amer. 576. 1932, pro parte. *Oenothera caespitosa* var. *eximia* sensu Munz, Amer. J. Bot. 18: 731. 1931, pro parte (as to plants from Colorado), non (A. Gray) Munz. Harrington, Man. Fl. Colo. 396. 1954, pro parte. *Oenothera caespitosa* subsp. *eximia* sensu Munz, N. Amer. Fl., Ser. II, 5: 100. 1965, pro parte (as to plants from Colorado), non (A. Gray) Munz.

Oenothera caespitosa Nutt. f. *caulescens* H. Lév., Monogr. Onothera 70. 1902, nom. nud.

Robust spring annual herb or rarely surviving for a second year in certain presumably favorable sites, from a stout taproot; stem simple or with 1–5 lateral stems from a definite basal rosette with reddish purple splotches on straw-colored background, rarely entirely straw-colored, 1.5–3 dm long, hirtellous, the hairs 0.6–1.6 mm long mixed with minute glandular hairs 0.1–0.2 mm

FIGURE 112. *Oenothera harringtonii*; El Paso Co., Colorado, isotype, *Ehlers 7461* (MICH).

long. Leaves closely spaced, green, thin, somewhat ascending, moderately hirtellous, with mixed glandular hairs, both types denser along the margins and midrib, narrowly oblanceolate, 10–14(–14.5) cm long, 1.5–2.3(–3) cm wide, acute at the apex, irregularly and coarsely dentate, the teeth triangular, 1–4 mm high or less, often a few larger lance-oblong rounded lobes 6–8 mm high near the base of the blade, the blade gradually tapering to a reddish purple or yellowish, broad petiole, 4.3–6.6 cm long. Buds erect without free sepal-tips. Flowers with a heavy sweet odor, generally 5–10 per stem opening per day, the floral platform nearly vertical. Ovary 11–14 mm long, densely hirtellous and glandular, sessile. Floral tube 3.1–6 cm long, ca. 1 mm diam. medially flaring to 7–11 mm at the mouth, densely hirtellous and glandular. Sepals green to yellowish green, the veins lightly infused with reddish purple pigment, acute at the apex, 1.7–2.6 cm long, 3–7 mm wide, hirtellous mostly along the midvein, occasionally also along the margins

and with glandular hairs dispersed more evenly over the surface. Petals fading pale pink, 2–2.6 cm long, 2.7–3.3 cm wide, the notch broad, 3–5 mm deep, glabrous. Staminal filaments 11–16 mm long; anthers 8–11 mm long. Style 6.5–9.6 cm long; stigma lobes 4.8–6.5 mm long, well elevated above or away from the stamens. Capsules 6–20 maturing per stem, obscurely quadrangular, straight, lanceoloid, (2.1–)2.5–3(–3.5) cm long, (5–)6–8 mm diam., tapering to a sterile beak 6–8 mm long, the free tips erect, 1.5–2 mm long; the margins of the valves with 5–8 conspicuous irregular tubercles, the tubercles 2–3 mm high, 2–4 mm apart, sometimes two or more are coalesced into a sinuate ridge, also with a medial ridge which is conspicuous for the length of the capsule, length of dehiscence ½–⅔ capsule length; pedicel 0.5–1 mm long, the base truncate, evenly pubescent with glandular hairs and sparsely hirtellous, glabrate in age. Seeds 60–100 per capsule arranged in 2 distinct rows or sometimes the rows partially overlapping, the raphe parallel or oblique to the plane of the capsular axis, narrowly obovoid, usually straight, reddish brown, sometimes spotted with yellowish waxy(?) layers which soon peel away, 2.1–2.3 mm long, 1–1.3 mm wide, 0.9–1.4 mm high; embryo portion contributing slightly less than ½ seed volume and projecting beyond the collar, the surface appearing finely striate but papillose under magnification; collar with its membrane intact at maturity, rarely splitting and separating from the collar, the collar margin entire. Self-incompatible. Gametic chromosome number, $n = 7$.

Distribution (Fig. 111). On compacted silty clays to looser rocky and sandy soils in open grasslands, known only from southeastern Colorado from western El Paso County and eastern Fremont County, southeast through Pueblo to Otero Counties, and south to Las Animas County, probably also in adjacent Colfax and Union Counties in New Mexico, 1,450–1,850 m. Flowering from mid-May through June.

Representative specimens examined. UNITED STATES. COLORADO: El Paso Co., Colorado Springs, *Jones 956* (G, POM); 4 mi. SE of Fountain, *Penland 1748* (US); S entrance to Ft. Carson, *Stockhouse 111* (MO); 9.5 mi. S of Fountain, Hwy. 125, *Stockhouse 137* (MO). Fremont Co., Hwy. 50 between Cañon City and Parkdale, 1957, *Barrell s.n.* (US); Cañon City Park, *Brandegee 830* (GH, NY, PH 2 sheets, UC, YU), 1877, *Brandegee s.n.* (UC); E of Concrete, Arkansas River Canyon, *Ewan 14195* (CAS, COLO, RSA); jct. Hwy. 115 & 120, *Stockhouse 112* (MO); 1 mi. E of jct. Hwys. 115 & 120, *Stockhouse 113* (MO). Huerfano Co., between Walsenburg and Pueblo, *Nelson 11527* (RM, UC). Las Animas Co., W of Mesa de Maya, Hwy. 160, *Rodgers 5751* (COLO, MICH, US); 29 mi. W of Kim, *Stephens & Brooks 22094* (DS, KANU); W of Trinchera, 1 mi. from New Mexico border, *Walter 1452* (ASU). Pueblo Co., Pueblo, 1897, *Bethel s.n.* (COLO), *Bethel 5101* (RM), *Christ 305* (ID), 1891, *Eastwood s.n.* (CAN, DS, NY, OSC), *Farwell 1051* (GH), 1873, *Greene s.n.* (NDG), *Robins 5022* (COLO), *Ripley & Barneby 7652* (CAS), *Rydberg & Vreeland 5858* (NY, RM); Arkansas River, near Pueblo, 1882, *Woodward s.n.* (GH, YU). Otero Co., Rocky Ford, Arkansas River, *Crandall 242* (GH, NY); N of Rocky Ford, *Osterhout 2085* (NY, RM); 25 mi. S of La Junta, *Paull 9* (COLO).

Most botanists have included this handsome species, distinctive in its robust leafy stems, subsessile capsules with large tubercles and 5–10 heavily scented flowers opening at one time, in their concept of *Oenothera eximia* [*O. caespitosa* var. *eximia* of Munz (1931b) and later authors]. The type of *O. eximia*, however, is a robust caulescent specimen of *O. caespitosa* subsp. *marginata* from Santa Fe, New Mexico. Munz's concept of *O. caespitosa* var. *eximia* seems to have been largely based on caulescence, so that he included plants of the caulescent annual we are describing here together with sporadic caulescent individuals of the perennial *O. caespitosa* (subspp. *marginata* and *macroglottis*).

Plants of *Oenothera harringtonii* consistently produce 6–20 capsules per stem, in contrast to the typically much lower numbers in *O. caespitosa*. The higher seed production in *O. harringtonii* is doubtless related to its derived annual habit. Goeken (1968) also reported that its flowers had a distinctive strong "gardenia-like" fragrance, different from the sweet fragrance of *O. caespitosa*. Pollination in *O. harringtonii* has not yet been observed.

Although *Oenothera harringtonii* is typically annual, some individuals, especially from the southern part of the range, appear to overwinter and flower for at least a second season [e.g., *Ewan 14195* (COLO), from Pueblo Co.; *Rogers 5751* (US) and *Stephens & Brooks 22094* from Las Animas Co.].

The range of *Oenothera harringtonii* overlaps with that of *O. caespitosa* subsp. *macroglottis* in Fremont County, Colorado, but because of their greatly different habitats, they rarely become sympatric. One area where they do come into contact is along the Arkansas River between Parkdale and Cañon City, where *O. caespitosa* subsp. *macroglottis* atypically occurs in a non-

FIGURE 113. *Oenothera cavernae*; Clark Co., Nevada, *Fisher 479* (RSA).

montane habitat along the river. Intermediates have not been observed.

This attractive species is named in honor of the late Harold D. Harrington (1903–1981), a longtime student of the Colorado flora, who made many critical collections from the state, especially the western half. His "Manual of the Plants of Colorado" (1954) remains the standard comprehensive floristic work for the state.

4. **Oenothera cavernae** Munz, Leafl. W. Bot. 3: 50. 1941. TYPE: Gypsum Cave, Sunrise Mountains, 18 mi. E of Las Vegas, 450 m, Clark Co., Nevada, 8 Apr. 1940, *Munz 16376* (holotype, POM-255352, photo MO; isotypes, BH, CAS, CS, DS, GH, MO, NA, RSA, UC, US, WS). Clokey, Univ. Calif. Publ. Bot. 24: 159. 1951. Munz, Calif. Fl. 950. 1959. Kearney & Peebles, Ariz. Fl. Ed. 2, 599. 1960. McDougall, Grand Canyon Wild Flowers 163. 1965. Munz, N. Amer. Fl., Ser. II, 5: 102. Raven, Madroño 20: 351. 1970. McDougall, Seed Pl. N. Ariz. 334. 1943. Lehr, Cat. Fl. Ariz. 109. 1978. Figure 113.

Winter or spring annual from a somewhat fleshy tapering taproot; acaulescent or with a central stem to ca. 4 cm long, usually with several lateral stems to ca. 3–4 cm long especially in robust individuals. Leaves forming a central rosette with smaller rosettes on the lateral stems if present, green to reddish green, lustrous, paler beneath, thin, usually with numerous scattered reddish purple splotches on the upper surface, pubescent with minute glandular hairs 0.12–0.2 mm long, sometimes also sparsely hirsute, the hairs 0.3–0.8 mm long, these rarely with an inconspicuous purple-pustulate base and mostly confined along or near the margins of the leaves or sometimes also along the major veins, oblanceolate to elliptic-oblanceolate in some exceptionally large leaves, lyrate-pinnatifid to nearly entire in very small individuals, (0.5–)2.5–13(–19.5) cm long, (0.2–)0.6–2.3(–2.7) cm wide, obtuse, rounded or rarely acute at the apex, the terminal lobe ovate to obovate, (0.6–)1–2.4(–2.9) cm long, (0.2–)0.6–1.5(–2) cm wide, the margins crenulate-denticulate to entire, rarely serrulate, the lateral lobes ca. 4–15 on each side of the winged petiole, angled slightly forward or at right angles to the midrib, lance-oblong, oblance-oblong, or sometimes the larger ones ovate-oblong, and the smaller ones deltoid or linear, the margin serrulate-denticulate to entire, rounded to some-

times acute at the apex, (0.5–)2–8(–11) mm long, (0.2–)0.5–2.5(–5) mm wide, the larger lobes usually alternating with smaller ones, tapering to a membranous winged petiole, 0.5–5.2 cm long. Buds without free sepal-tips, sometimes somewhat recurved before anthesis. Flowers 1–3(–10) opening per day, without noticeable scent. Ovary 4–8 mm long, sessile, evenly and sparsely hirsute with a mixture of glandular hairs, one hair type dominating over the other in some populations. Floral tube whitish, (2–)3–3.7(–4.7) cm long, 0.6–1.2 mm diam. medially, flaring to 5–6.2 mm at the mouth, moderately pubescent with glandular hairs and also sparsely hirsute. Sepals green and with numerous reddish purple splotches, 4.5–12 mm long, 2–4 mm wide, pubescent adaxially in the same manner as the floral tube. Petals fading to a pale pink, (6.5–)8–20(–25) mm long, (5–)7.5–19(–27) mm wide, the notch 2–5 mm deep, glabrous or rarely with a few widely scattered glandular hairs. Staminal filaments 5.2–7.5(–12) mm long; anthers (1.4–)3–4.5(–6) mm long, shedding pollen directly on the stigma after the flower opens. Style (2.4–)3.5–4.5(–5.6) cm long; stigma lobes pale greenish yellow, 2.3–3.2 mm long, often erect and coherent at anthesis but typically separating in age. Capsules 1–40 per plant, elliptic ovoid to ovoid, obscurely quadrangular, falcate especially before maturity, 1.2–3.8 cm long, 6–14 mm diam., tapering to a sterile beak 2–8 mm long, the free tips 0.4–1.3 mm long, recurved, pubescent evenly with glandular hairs and sparsely hirsute, the hairs evenly scattered, the margins of the valves with a sinuate ridge or 8–20 nearly distinct tubercles, the tubercles 0.3–0.7 mm high, 1–3(–4) mm apart, the capsule drying to a hard woody texture, dehiscing ⅓–½ its length; sessile or rarely on a pedicel to 1 cm long, the base when the capsules are crowded, seeds 5–80 per capsule, arranged in two adjacent rows per locule, the raphe parallel to the plane of the capsular axis, obovoid sometimes curved, brown, 2.5–3.1 mm long, 1.1–1.4 mm wide, 1.2–1.6 mm high; embryo portion constituting about ½ of the seed; seed-collar without a membrane, producing a large empty cavity, the margin of the collar irregularly sinuate, the seed surface minutely papillose to reticulate. Self-compatible and autogamous. Gametic chromosome number, $n = 7$.

Distribution (Fig. 111). On exposed calcareous slopes, along crevices in limestone, dolomite, or loose tallus, and along sandy arroyos and sandstone, granitic crevices, or volcanic cinders in Mojave Desert or Great Basin scrub communities, rarely in arid phases of juniper woodland from the Sheep, Las Vegas, and Arrow Canyon ranges and the low hills near Arden and Sloan in Clark County, Nevada east along the Grand Canyon to the vicinity of Page, Arizona, and perhaps Washington County, Utah and formerly in Glenn Canyon, 450–1,700 m. Flowering March to May, after rains.

Representative specimens examined. UNITED STATES. ARIZONA: Coconino Co., Grand Canyon, rim of Little Colorado River, *Aitchison 4* (MNA); Grand Canyon, Marble Canyon, Navajo Bridge, *Benson 138* (UC); Grand Canyon, Bright Angel Trail, 1938, *Darrow s.n.* (ARIZ); Havasu Canyon, Hualapi Trail, *Deaver 1305* (ASC, CAS); Havasu Canyon, Mooney Falls, *Deaver 3522* (ASC, MNA); Grand Canyon, Hermit Trail, *Eastwood 5970* (CAS); Grand Canyon, 10 mi. N of Navajo Bridge, 1942, *Cantelow s.n.* (CAS); Grand Canyon, 1–1.5 mi. N of Navajo Bridge, 1942, *Cantelow s.n.* (CAS); Lees Ferry, 1890, *Jones s.n.* (POM); Marble Canyon, Harding Rapids, Ferry, 1890, *Jones s.n.* (POM); Marble Canyon, Harding Rapids, 1974, *Niemer s.n.* (ASC); Grand Canyon, Shinumo Rapids, 1973, *Phillips s.n.* (ASC); Grand Canyon, Cardenas Creek, 1973, *Phillips s.n.* (MNA, ARIZ); Grand Canyon, Buckfarm Canyon, *Theroux 1287* (MNA). Mojave Co., Grand Canyon, Virgin Narrows, *Atwood & Higgins 4524* (BRY, MO, WTS); Grand Canyon, Vulcans Throne, *Cottam 12918* (RSA, UT); Grand Canyon, Vulcans Throne, *McClintock 52-188* (CAS); Grand Canyon, Toroweap Valley, *McClintock 52-578* (CAS); Grand Canyon, Colombine Falls, *Phillips 75-33* (ARIZ); Lake Mead Natl. Rec. Area, Lower Granite Gorge, 1973, *Van Devender et al. s.n.* (ARIZ). NEVADA: Clark Co., Fossil Ridge, *Ackerman & Berger TA6308* (UNLV); Spring Mts., above Arden, *Barneby 2885* (CAS, POM); Arrow Canyon Range, *Fisher 479* (RSA); West End Wash, Anniversary Mine, *Holland 877* (UNLV); 7 mi. SW of Las Vegas, *Munz et al. 22996* (UC, CAS); Sheep Mt., near Jean, *Ripley & Barneby 3327* (POM, NY, UC); 20.7 mi. NE of N Las Vegas, *Raven 11810* (RSA); Sunrise Mt., Gypsum Cave, *Wagner 3994* (MO); vicinity of Anniversary Mine, West End Wash, *Wagner 3998* (MO); Jean, S of prison, *Wagner 3992* (MO); Desert Nat'l. Wildlife Range, SE end of Las Vegas Range, SW of Gass Peak, *Wagner 3999* (MO); 9.6 mi. SW of jct. I-15 and Hwy. 7 on I-15, *Wagner 4595* (MO). Lincoln Co., Meadow Valley Mts. (T13S, R64E, Sec. 6), *Tiehm 6854* (MO, RENO). UTAH: Washington Co., near St. George, *Parry 65* (G, GH, MO, PH). San Juan Co., Glen Canyon, 2 mi. below Last Chance Creek, *Gaines 981* (MNA, WS); without locality, 1972, *Capt. Bishop s.n.* (US).

Oenothera cavernae is a distinctive species restricted to very arid slopes, usually on limestone or along desert arroyos. Most distinctive are the characteristics of its leaves. The pattern of alternating large and small leaf lobes with typically rounded apices gives a distinctive irregular appearance to the leaves reminiscent of the leaf lobing in *O. primiveris* but also resembling some

TABLE 15. Comparison of characters in *Oenothera brandegeei, O. cavernae,* and *O. caespitosa* subsp. *crinita.*

Character	*O. caespitosa* Subsp. *crinita*	*O. brandegeei*	*O. cavernae*
Habit	Perennial	Annual	Annual
Petal length (mm)	16–35	8–16	6–20
Stigma position	Elevated above anthers	Surrounded by anthers	Surrounded by anthers
Genetically self-compatible	Yes	No	No
Apex of leaf lobes	Acute to rarely rounded	Acute	Usually rounded
Capsule			
Number of tubercles/valve	8–15 or sinuate ridge	4–7	8–20 or sinuate ridge
Height of tubercles (mm)	0.3–1.5	1–1.5	0.3–0.7
Length of dehiscence	⅓–½	⅔	⅓–½
Seed			
Collar	Closed or open cavity, thin layer cellular matrix, ribbed	Collar walls rolled outward, cavity filled with cellular matrix, ribbed	Open cavity, hollow, ribbed
Surface	Papillose to reticulate, rarely irregularly roughened	Irregularly roughened	Papillose to reticulate

populations of *O. caespitosa* subsp. *crinita* such as *Beatley 7709* from Nye County, Nevada, *Phillips 76-58* from Clark, County, Nevada, and *Maguire & Holmgren 21840* from Toole County, Utah. The reddish pigment commonly present in the leaves is likewise unique in this section, whereas the regularly occurring and conspicuous reddish purple splotches also occur on the young leaves of *O. brandegeei* and *O. caespitosa* subsp. *navajoensis,* and sporadically on mature leaves in some populations of *O. caespitosa* subspp. *marginata* and *crinita.* The conspicuous reddish purple splotches on the flower buds in *O. cavernae* are also found in some populations of *O. caespitosa* subsp. *crinita* and occasionally in populations of subsp. *marginata.*

Oenothera cavernae and *O. brandegeei* are annuals with relatively small self-pollinating flowers in which the stigma lobes are often erect at anthesis. These similarities caused Munz to annotate a specimen of *O. cavernae* (1872, *Capt. Bishop s.n.*) from Utah as "*O. caespitosa* var. *brandegei*" a decade before he realized that the northern plants represented a different and undescribed species. There are other features of the leaves, capsule, and seed (Table 15), however, that clearly show that *O. cavernae* and *O. brandegeei* are each more closely allied to *O. caespitosa* subsp. *crinita* than they are to each other. The annual habit and autogamy have been, therefore, independently derived in the evolution of both species and are closely linked to their ephemeral existence in an unpredictable and arid environment as first suggested by Raven (1970).

In spite of the limited range of habitats occupied by *Oenothera cavernae,* this species exhibits a considerable morphological variation, that is evidently mostly related to the seasonal availability of moisture. Other differences between plants, such as flower size, which has a geographical component, have evidently been fixed by autogamy at least in part. In part, petal size varies within a population or even a single individual and also appears to correlate with crowding or water stress. But, in general, plants of *O. cavernae* from the eastern part of the range have larger flowers (e.g., 1973, *Phillips s.n.* with petals to 25 mm long). At the western end of the Grand Canyon plants with petals as short as 6 mm long have been collected (e.g., *Phillips 75-33*), while most plants from Clark County, Nevada have petals of intermediate lengths (12–16 mm long).

The range of *Oenothera cavernae* overlaps with that of *O. caespitosa* subsp. *crinita* to which it is most closely related, and also with subspp. *mar-*

ginata and *navajoensis,* but because of their differing edaphic requirements, these never grow together.

5. Oenothera brandegeei (Munz) Raven, Madroño 20: 352. 1970. Wiggins, Baja Calif. 753. 1980. *Oenothera caespitosa* Nutt. var. *brandegei* Munz, Amer. J. Bot. 18: 732. 1931. TYPE: Stone ridges, Bahía de los Angeles, Baja California, Mexico, Dec. 1887, *Palmer 582* (holotype, GH, photo MO; isotype, US). The mention of *Palmer 542* by Munz (1931b) and Raven (1970) as the type of this species was a misinterpretation of the number on the label which is actually *Palmer 582.* According to Sereno Watson's account (1889) of Palmer's trip in 1887, *Palmer 542* was a specimen of *Psorothamnus emoryi* (A. Gray) Rydb. Wiggins, Fl. Sonoran Desert II, 2: 1051. 1964. *Oenothera caespitosa* Nutt. subsp. *brandegei* (Munz) Munz, N. Amer. Fl., Ser. II, 5: 101. 1965. Figure 114.

Winter or spring annual from a slender taproot; acaulescent or rarely with a single stem to ca. 3 cm long. Leaves forming a rosette, dull green, thin, sparsely hirsute mostly along the margins, the hairs 0.3–0.8 mm long mixed with minute glandular hairs 0.14–0.2 mm long, sometimes with conspicuous whitish bundles of raphides scattered near the surface of broad leaves, young leaves often with conspicuous reddish purple splotches fading with age, oblanceolate to very narrowly oblanceolate in outline, 3.5–13.7 cm long, 0.1–3.1 cm wide, lyrate-pinnatifid or -pinnatisect in robust plants to merely pinnatifid, bipinnatifid, or serrate in small individuals, acute at the apex, the terminal lobe if present ovate, 2–4.5 cm long, 1.6–3.1 cm wide, the margin dentate to serrate, the lateral lobes 6–33 on each side of the winged petiole, angled forward, to nearly perpendicular, linear to oblong-lanceolate or oblong, the smaller lobes deltoid, acute at the apex, the margin dentate, serrate, or entire, 0.1–17 mm long, 0.1–4 mm wide, the membranous winged petioles 0.8–7 cm long. Buds erect. Flower without noticeable scent, fading pink, generally 1–3 opening per day. Ovary 0.5 cm long, sessile, evenly glandular pubescent. Floral tube 0.5–4 cm long, ca. 1.4 mm diam. medially, flaring to 5 mm at the mouth, moderately hirsute. Sepals green, 5–12 mm long, 0.7–3.5 mm wide, sparsely hirsute, mostly on the midvein and margins and also with scattered erect glandular hairs. Petals fading pink, oblanceolate to narrowly obovate, 8–16 mm long, 4.5–15 mm wide, glabrous or very sparsely hirsute, the few hairs near the margins. Staminal filaments 5–8 mm long; anthers pale yellow, 3–5 mm long, shedding pollen directly on the stigma at anthesis. Style 1–4.8 cm long; stigma lobes 2–5 mm long and often erect and coherent at anthesis. Capsules 1–30 per plant, ovoid, terete falcate at least when young, 0.6–1.9 cm long, 3–7 mm diam., tapering to a sterile beak 3–7 mm long, the free tips 0.5–2 mm long, evenly glandular pubescent and sparsely hirsute, the valves with 4–7 tubercles along the margin, the tubercles 1–1.5 mm high, 1–3 mm apart, the capsule drying to a hard woody texture, length of dehiscence about ⅓ capsule length; sessile or on a pedicel 0.5–1 mm long. Seeds irregularly triangular in outline sometimes somewhat curved, dark reddish brown, 2.5–3 mm long, 1.6–2.5 mm wide, 1–30 per capsule arranged in 2 rows in each locule, the two rows partially overlapping, the raphe oriented at various angles to the plane of the axis of the capsule; seed-collar broadly tri-

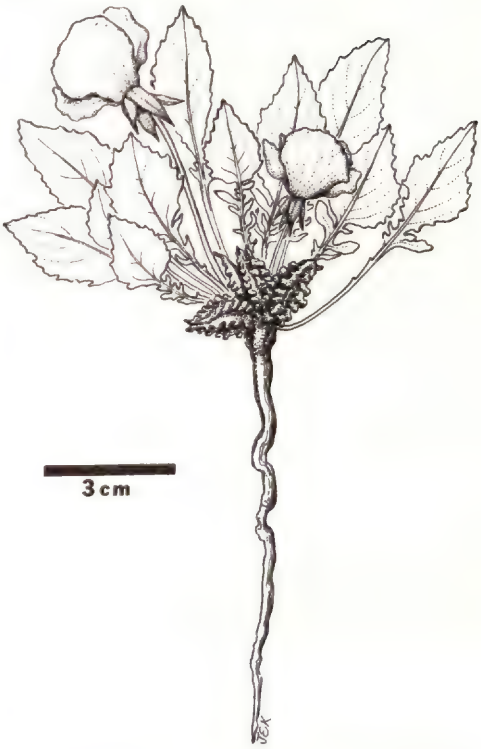


FIGURE 114. *Oenothera brandegeei*; Baja California, isotype, *Palmer 582* (US).

angular, constituting slightly less than ½ of the seed, the seed-collar margins rolled outward, the exposed cavity filled with large empty golden brown cells derived from the outgrowths, the entire structure with a narrow groove obscuring the raphe, the margin obscurely sinuate, the seed surface minutely roughened. Self-compatible and autogamous. Gametic chromosome number, $n = 7$.

Distribution (Fig. 111). On arid rocky slopes of the mountains near Bahía de los Angeles, and among volcanic rocks on the mountains of Isla Angel de la Guarda east of Bahía de los Angeles in the Golfo de California. Flowering December to May, after rains.

Additional specimens examined. MEXICO. BAJA CALIFORNIA: Isla Angel de la Guarda, N slope of peak SW of Pond Island, 350 m, *Moran 12983* (SD); cultivated at CS from *Moran 12983*; 1972, *Stockhouse s.n.* (MO).

Oenothera brandegeei is a very specialized member of the *O. caespitosa* group. Its principal distinguishing features are its small self-pollinating flowers, annual habit, the leaves which are usually divided into narrow divisions that typically are angled forward, and the seed-collar filled with a matrix of large cells. Other features, however, such as leaf size, number and size of leaf lobes, capsule size, and seed number are highly variable, even when plants grown from seed of the Isla Angel de la Guarda population are grown in the greenhouse with ample water, they never attain the stature of the Bahía de los Angeles plants, of which we have been unable to obtain living material, nor do they have the broadly ovate terminal lobe found in those plants. Raven (1970) concluded that, despite these differences, the two populations should be maintained as one species.

Oenothera brandegeei and *O. cavernae* are both autogamous annuals with small flowers, but they differ in many features. *Oenothera brandegeei* has a seed-collar that is filled with a cellular matrix (Fig. 93), narrow acute leaf lobes, large tubercles, and capsules that dehisce about two-thirds their length; *O. cavernae* has an open sinuate margined seed-collar that forms an empty cavity (Fig. 60), rounded leaf lobes, small tubercles, and capsules that dehisce from one-third to one-half their length. Moreover, these features of *O. cavernae* ally it most closely to certain low-elevation populations of *O. caespitosa* subsp. *crinita* rather than to *O. brandegeei*. For a more detailed comparison see the discussion under *O. cavernae*.

EXCLUDED SPECIES

Oenothera brachycarpa A. Gray, Pl. Wright. 1: 70. 1852. The type as well as all of the material referred to the following entity by Munz (1931b) is the yellow-flowered *O. brachycarpa* A. Gray in sect. *Megapterium*. *Pachylophus australis* was described in error as having white flowers.

Pachylophus australis Woot. & Standl., Contr. U.S. Natl. Herb. 16: 156. 1913. TYPE: S fork of Tularosa Creek, Sacramento Mts., Otero Co., New Mexico, 1,800 m, 31 July 1897, *Wooton s.n.* (holotype, US-690245, photos MO, NMC). According to Wooton's 1897 field notes at New Mexico State University, he was collecting on the S fork of Tularosa Creek on 31 July 1897 (R. Spellenberg, pers. comm.). The label on the type specimen, however, gives 1899 as the year of collection. Wooton's 1899 field notes were unavailable, but it seems most likely that the wrong year was written on the label, especially since the name was not published for over a decade after the specimen was collected. *Oenothera australis* (Woot. & Standl.) Tidestrom in Tidestrom & Kittel, Fl. Ariz. & N. M. 277. 1941. *Oenothera caespitosa* Nutt. var. *australis* (Woot. & Standl.) Munz, Amer. J. Bot. 18: 733. 1931. *Oenothera caespitosa* subsp. *australis* (Woot. & Standl.) Munz, N. Amer. Fl., Ser. II, 5: 101. 1965.

DOUBTFUL NAME

Oenothera caespitosa Nutt. f. **albiflora** H. Lév., Monogr. Onothera 70. 1902. We have been unable to find authentic material of this entity. Léveille's description is far too brief to accurately determine the identity of this taxon.

APPENDIX

NATURAL HYBRIDIZATION BETWEEN THE SUBSPECIES OF *OENOTHERA CAESPITOSA*

Hybrids involving subsp. crinita. *Oenothera caespitosa* subsp. *crinita* grows in the same areas as subsp. *marginata* throughout much of its range, and in the same region as subsp. *caespitosa* in

TABLE 16. Character differences among *Oenothera caespitosa* subsp. *marginata*, subsp. *crinita*, and presumed derivatives from Blue Mountain, Humboldt Co., Nevada.

	Subsp. *marginata*	Presumed Hybrid	Subsp. *crinita*
Leaf length (NV only) (cm)	8–36	9.5–22	2.5–16.5
Floral tube length (cm)	7.5–16	5.3–10.5	2.8–7.5
Color of faded petals	Pink	Pink to lavender	Rose to rose purple
Length of hirsute hair type (mm)	0.5–2.2	0.6–1.2	0.5–1.5
Capsule length (cm)	(2.1–)2.5–5.5(–6.8)	2.5–4.5	1–3(–3.4)
Capsule shape	Cylindrical to lance-cylindrical, nearly straight	Lance-cylindrical curved to falcate	Elliptic-ovoid to lanceoloid falcate or sigmoid
Capsule cross-section	Nearly terete	Flattened	Flattened
Rows of seeds per locule	2	1	2
Seed-collar	Entire to rarely slightly sinuate, not ribbed	Sinuate margin, ribbed	Sinuate margin, ribbed

northern Nevada (Fig. 100). Within these areas the common form of subsp. *crinita* comes into marginal contact with the other entity. In general, subspp. *marginata* and *caespitosa* occur in montane sites in this area. Subspecies *crinita* occupies rocky slopes and arroyo margins in Mojave or Great Basin desert scrub up to pinyon-juniper woodlands on the upper bajadas and in the lower canyons. Thus subsp. *crinita* may grow with the others at its upper elevational limit. At these sites of marginal contact, the entities appear to hybridize readily or to have hybridized in the past. Subsequently this has led either to stabilized hybrid populations with one or neither putative parent currently present in the area, or to various kinds of large hybrid swarms that contribute to a gradual transition from one subspecies to the other.

The intermediates between *Oenothera caespitosa* subspp. *marginata* and *crinita* occur mostly in habitats similar to those occupied by subsp. *crinita*, which they resemble. They do not, however, appear to be restricted solely to zones of overlap, but have even been collected at the lower elevation limits of subsp. *crinita* where subsp. *marginata* is not known to occur. In contrast, the intermediates between subspp. *crinita* and *caespitosa* occur in variable low elevation desert scrub populations that are morphologically more similar to those of subsp. *caespitosa*. Montane populations of subsp. *caespitosa* in these areas, however, apparently remain unaffected. The pulvinate form of subsp. *crinita* does not hybridize with any of the other subspecies with the one possible exception in Kane County, Utah, mentioned in the taxonomic treatment under subsp. *crinita*.

Intermediate populations or individuals have been categorized in various ways. First they have been included with the putative parent that they most closely resemble and are grouped secondarily as to whether they appear to represent hybrid derivative populations that have replaced their putative parent or more sporadic hybrid individuals or populations with the putative parents present. The following appear to be stabilized intermediate population series:

1. Variable plants from the floodplain of a wash on the southeast side of Blue Mountain in Humboldt County, Nevada (*Holmgren & Holmgren 3986*, ARIZ, ASU, BRY, CAS, ID, NY, UMO, UNLV, US, UT, UTC, WTS) have features of both *Oenothera caespitosa* subspp. *crinita* and *marginata*, but are most similar to subsp. *marginata* (Table 16). The putative parents are not known from the area, but the region has not been well collected.

2. Populations of *Oenothera caespitosa* subsp. *marginata* from Lee and Kyle Canyons in the Charleston Mountains, Clark County, Nevada, are extremely variable in leaf and flower size. The plants also have broader capsules than usual for subsp. *marginata*, but the seeds are typical in all respects. Shorter leaves, shorter floral tubes, and broader capsules suggest that populations of subsp. *marginata*, which occur on limestone in

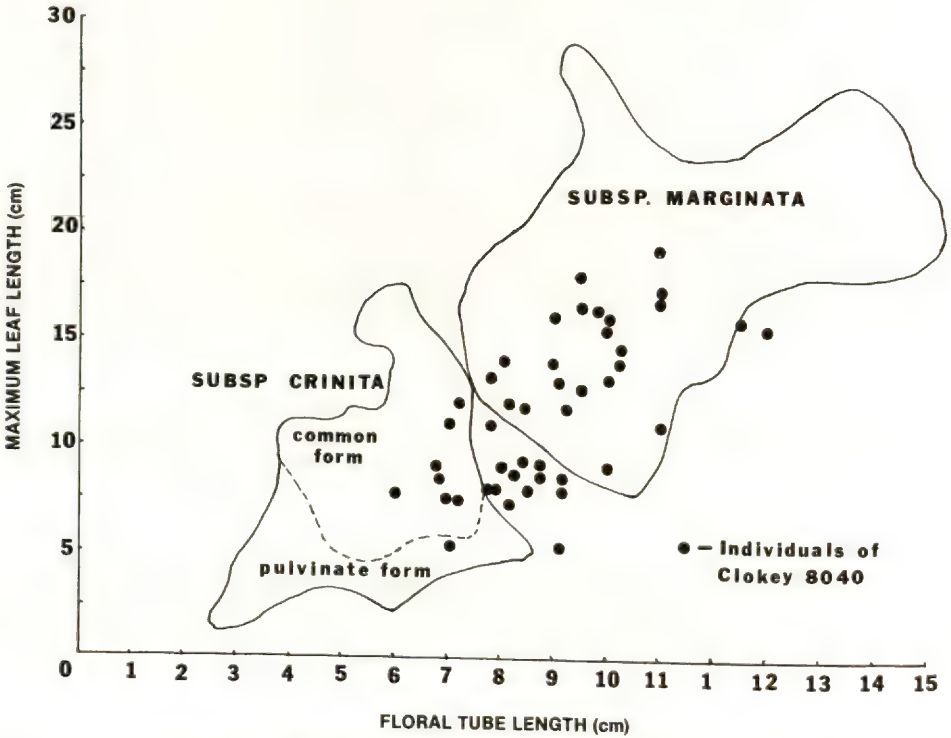


FIGURE 115. Comparison of maximum leaf length and floral tube length of a population, *Clokey 8040*, from the Charleston Mountains to the overall ranges of *Oenothera caespitosa* subspp. *marginata* and *crinita* from Utah, Nevada, and California.

the canyon bottoms and lower slopes, have hybridized in the past with subsp. *crinita*, which occurs at higher elevations on crumbly soils and rocky ridges. Floral tube lengths and maximum leaf length for 45 individuals of one population (*Clokey 8040*) from Lee Canyon were measured and are plotted in Figure 115. The full ranges of subspp. *crinita* and *marginata* (from other California, Nevada, and Utah localities) are also shown for comparison. The Lee Canyon population is clearly atypical and intermediate between the two subspecies in these characters.

3. Plants from the Pyramid-Winnemucca Lake region, Nevada, are intermediate between subspp. *crinita* and *marginata* in floral tube length but are unique in their narrow forward-pointing lobes. They are also densely glandular-pubescent but lack any other hair type. They have the seed morphology of subsp. *marginata*. The origin of these perplexing plants has perhaps involved hybridization between subspp. *marginata* and *crinita* (see further discussion of them in the taxonomic section under subsp. *marginata*).

Some plants appear to be exactly intermediate while more commonly they resemble one subspecies more than the other. In classifying individual specimens certain features were given precedence over others. Those features emphasized for intermediates with *Oenothera caespitosa* subsp. *marginata* were seed and capsular morphology (when available) and secondarily maximum leaf length, floral tube length, and color of the faded petals. For intermediates with subsp. *caespitosa*, the type and length of hairs coupled with seed morphology and presence or absence of glandular hairs were stressed. The result of using these criteria has been to place most of the specimens with some intermediate features between subspp. *marginata* and *crinita* into subsp. *crinita*, whereas those intermediate with subsp. *caespitosa* were mostly placed in that subspecies.

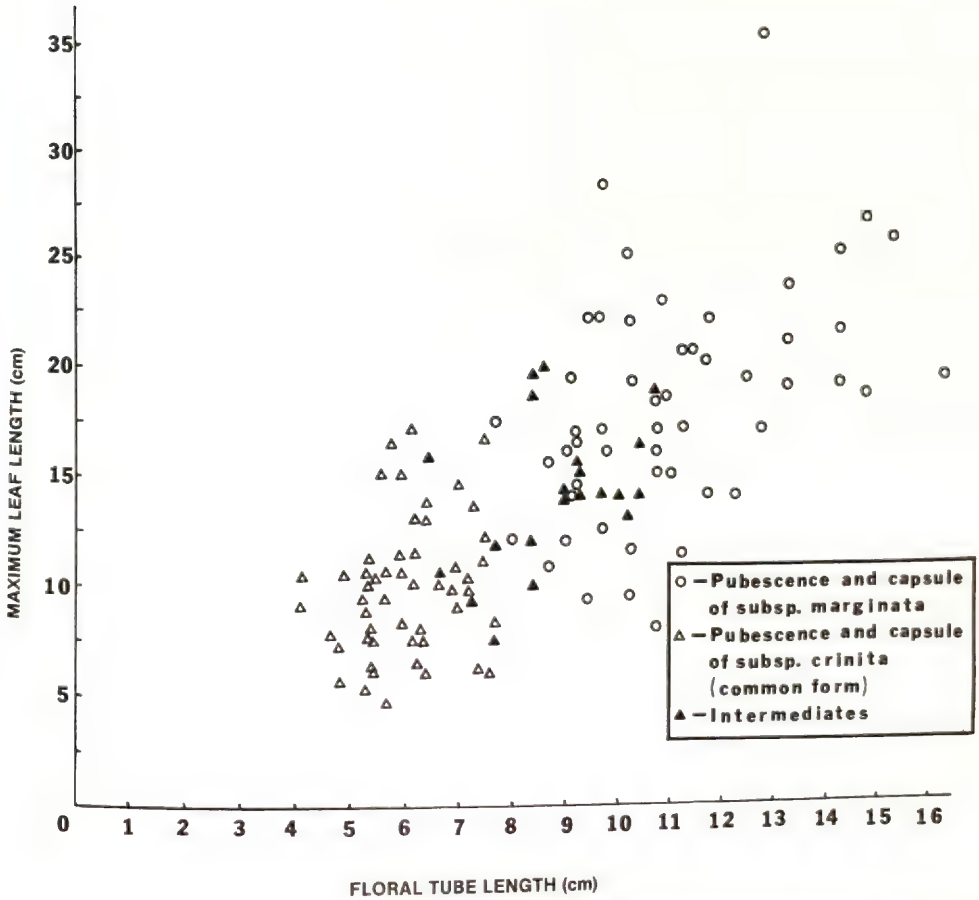


FIGURE 116. Comparison of morphological features of Utah, Nevada, and California plants of *Oenothera caespitosa* subspp. *marginata* and *crinita*.

Two series of populations involving intergradation with *Oenothera caespitosa* subsp. *marginata* will now be discussed, followed by the discussion of one involving intergradation with *O. caespitosa* subsp. *caespitosa*.

1. Many populations centering in eastern Tooele County and Salt Lake County, around the Great Salt Lake, have capsule, seed, and to some extent leaf features that are well within the range of *O. caespitosa* subsp. *marginata*. Other collections, however, mostly from an area bound by Salt Lake City south to Sandy and west to the Stansbury Mountains (e.g., *Jones 1746* from Salt Lake City; 1884, *Leonard s.n.*, from Sandy) often have shorter floral tubes than normal (5–8 cm long, mean 7.5 cm long), densely pubescent, short leaves 8–12 cm long, and nearly sessile capsules. All of these features are suggestive of *O. caespitosa* subsp. *crinita*, and they may have resulted from past hybridization. Alternatively, as discussed in the taxonomic section under subsp. *marginata*, the shorter floral tubes and leaves may be related to the south-to-north cline in the length of these features in that subspecies.

2. A series of populations in and between the Panamint and Inyo Mountains in Inyo County, California, contains many diverse intermediates between *O. caespitosa* subspp. *crinita* and *marginata*. In this area, subsp. *marginata* occurs primarily from pinyon-juniper woodland to pine forests, whereas the common form of subsp. *crinita* is found from blackbrush scrub up to pin-

yon-juniper woodlands. The intermediates are mixed predominantly with populations of subsp. *crinita* and appear to have a similar ecological range. Extensive hybridization appears to have altered the pattern of variation in the populations of subsp. *crinita* from this area considerably. There is a similar pattern in populations in northern San Bernardino County, California, and Clark and Nye Counties, Nevada, but in these areas the intergradation seems to be considerably less extensive. Unfortunately we have not yet had an opportunity to gather detailed information in any of these populations. The general pattern, however, can be ascertained by comparing the full ranges of variation in floral tube and maximum leaf length coupled with capsule and seed morphology from herbarium material of subsp. *marginata,* subsp. *crinita,* and the intermediates (Fig. 116). Undoubtedly the contrast between the two subspecies and intermediates would be greater if individual populations were studied.

The intermediate plants are much more variable than either parent. In some of them the capsules and seeds are virtually indistinguishable from those of subsp. *crinita,* whereas the floral tubes and leaves are much longer than those of subsp. *crinita* and are similar to those of subsp. *marginata.* In others, the capsules are intermediate, but the floral tubes and leaves may fall within the normal range of subsp. *crinita.* Sometimes the plants have combinations of features from both parents such as the capsule shape and seed morphology of subsp. *crinita* and the long pedicel of subsp. *marginata.* Seeds of intermediate morphology have not been found.

Much more ambiguous is a series of populations in northern and central Arizona and the San Bernardino Mountains in southern California. These plants are, at least superficially, more similar to the Idaho and Oregon plants of subsp. *marginata* than they are to surrounding populations of subsp. *marginata,* especially in their short leaves and floral tubes.

The first series of Arizona populations are restricted to volcanic cinders around Sunset Crater in north-central Arizona. The other Arizona series is from areas near Prescott 170 km to the southwest, and the San Bernardino County, California, series is from Big Bear Valley about 350 km west of Prescott. The Sunset Crater plants have small, linear-oblanceolate, pinnately-lobed leaves 5–11 cm long that are hirsute and glandular pubescent, floral tubes 5–6 cm long that are flecked with reddish purple spots as are the sepals, nearly sessile oblanceoloid capsules 1.3–2.6 cm long and seed features typical of *Oenothera caespitosa* subsp. *marginata.* The Prescott plants are more variable than the Sunset Crater populations with floral tubes mostly 6–7(–9) cm long. Their leaves and capsules are larger than those from Sunset Crater, with some in the range typical of *O. caespitosa* subsp. *marginata.* The San Bernardino Mountain plants also present a similar overall range of variation with leaves and floral tubes 6.6–8 cm long. Both the Prescott and San Bernardino plants have reddish purple spotted buds and floral tubes. Based on maximum leaf length versus floral tube length coupled with capsule morphology, the Sunset Crater populations are intermediate between *Oenothera caespitosa* subspp. *navajoensis* and *marginata* (Fig. 117, enclosed by the dotted line) and may represent a stabilized hybrid derivative that colonized these elevationally intermediate volcanic cinder sites. This explanation, however, does not seem likely for the Prescott and San Bernardino plants because they are so far removed geographically from the range of *O. caespitosa* subsp. *navajoensis.* Alternatively, it is possible that *Oenothera caespitosa* subsp. *crinita* may have been involved in the formation of the Prescott and San Bernardino populations. Plants included in subsp. *crinita* from Mohave County, Arizona, are superficially similar to them, but differ in that they have the distinctive elliptic-ovoid capsules, low tubercles, and the two-toned colored seeds with ribbed collars characteristic of subsp. *crinita.* Thus they are within the normal range of variation for subsp. *crinita,* except that their leaves approach those of subsp. *marginata* in their lobing and in being less pubescent.

Because of the great similarity in the phenotypes, it is impossible at least with current knowledge of these three populations to differentiate between the following hypotheses: (1) that all three populations originated via hybridization between subspp. *marginata* and *navajoensis* followed by stabilization of the derivatives; (2) that hybridization events involved in some way both subspp. *navajoensis* and *crinita* with subsp. *marginata*; or (3) that they are populations that merely have retained primitively short, reddish spotted floral tubes while becoming specialized vegetatively.

Hybrids involving subsp. caespitosa. The range of *Oenothera caespitosa* subsp. *caespitosa*

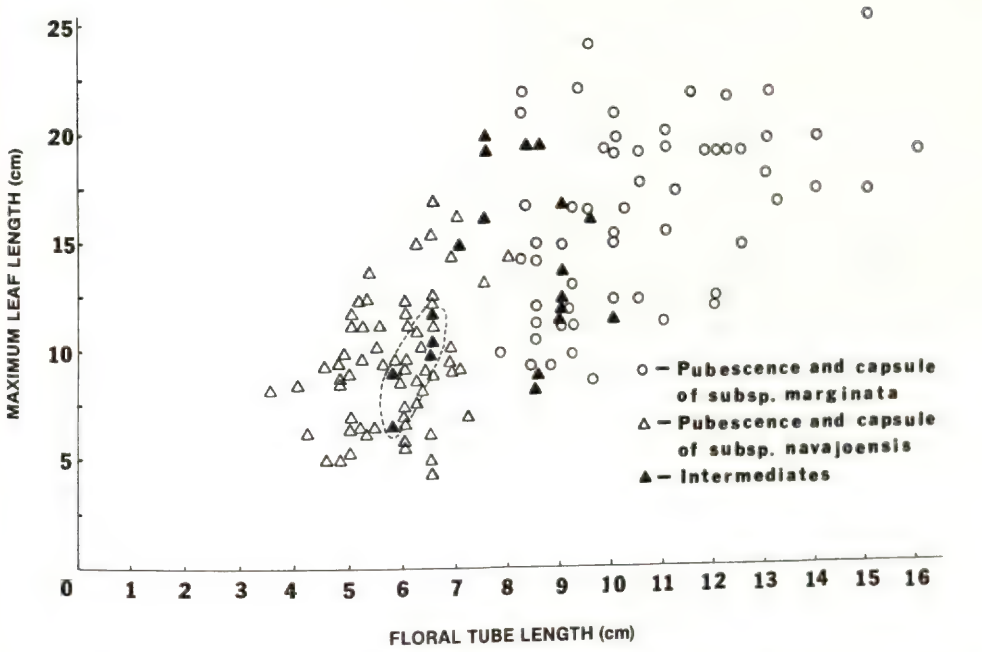


FIGURE 117. Comparison of morphological features of Utah, Colorado, Arizona, and New Mexico plants of *Oenothera caespitosa* subspp. *marginata* and *navajoensis*.

overlaps that of subspp. *macroglottis, marginata,* and *crinita*. Intermediates or plants presumed ultimately to have had a hybrid origin are known within or adjacent to each of the areas of range overlap. The overall pattern of intergradation is different with each of the subspecies as follows:

1. *Oenothera caespitosa* subsp. *marginata* has an extensive region of geographical overlap with subsp. *caespitosa,* the broadest zone of overlap in the *O. caespitosa* group. Throughout this large area the two subspecies are edaphically separated, subsp. *marginata* occurring primarily on sandy or coarse soils, and subsp. *caespitosa* primarily on clays and shales. Throughout their area of overlap only sporadic hybrids or localized hybrid derivative populations appear to have been produced.

2. The range of *Oenothera caespitosa* subsp. *macroglottis* overlaps broadly with that of subsp. *caespitosa* over the northern third of Colorado. They are edaphically isolated like subspp. *caespitosa* and *marginata*. The long-haired populations of subsp. *caespitosa* (discussed on p. 41) have features similar to those in subsp. *macroglottis,* and were presumably derived following past hybridization. No other evidence of hybridization was found.

3. The area occupied by intermediate populations between *Oenothera caespitosa* subspp. *caespitosa* and *crinita* centers in Humboldt and Elko Counties in northern Nevada, where the plants occur in Great Basin scrub communities. The populations are phenotypically diverse, and include a broad array of phenotypes that combine characteristics of both subspecies, but neither extreme is represented. Most frequently the individuals had features of subsp. *caespitosa* but also had glandular hairs on the floral tubes or some longer or spreading hairs scattered on various parts of the plant. Other plants were variable, with erect hairs 0.3–1.2 mm long and an understory of glandular hairs. This range of pubescence lengths encompasses the entire combined ranges for both subspp. *caespitosa* and *crinita*. On the other hand, plants that fall into the range of subsp. *crinita* for most characters often had thicker somewhat appressed hairs and less flattened capsules.

Both subspecies in their more typical form, however, do occur in the region. Moreover, these populations of both subspecies do not show any

evidence of past or present hybridization. Populations with characteristics typical of *Oenothera caespitosa* subsp. *caespitosa* occur on limestone outcrops generally above 2,400 m in many of the isolated mountains of northern Nevada. In sharp contrast to the predictable occurrence of these populations of subsp. *caespitosa,* subsp. *crinita* is represented only by scattered populations in desert habitats similar to those occupied by the intermediates as well as in pinyon-juniper woodlands. The variable populations of intermediates are presumably the result of extensive hybridization between once more widespread populations of subspp. *caespitosa* and *crinita* since the close of the last pluvial period some 10,000 years ago. Low-elevation populations of both subspecies apparently were largely replaced in the drier areas.

Populations at low elevations in adjacent Oregon northward to the John Day River near Clarno, Wheeler County (*Wagner 4466*) are a close match to most populations of subsp. *caespitosa,* but the presence of glandular hairs on young leaves, floral tubes, and cotyledons and their proximity to the intermediates in Nevada between subspp. *caespitosa* and *crinita* suggests that they are perhaps hybrid derivatives that have colonized this region since the close of the last pluvial period. Other than the glandular hairs, they are virtually indistinguishable from subsp. *caespitosa* from farther east.

Hybrids involving subsp. navajoensis. The range of *Oenothera caespitosa* subsp. *navajoensis* overlaps that of subsp. *marginata* over a wide region. It also overlaps that of subsp. *macroglottis* in Montrose, Delta, and Montezuma Counties in Colorado and in areas around the LaSal Mts., Grand County, Utah. Subspecies *macroglottis* grows at higher elevations in montane forests on the plateaus and in the mountains, whereas subsp. *navajoensis* occurs at much lower elevations. This ecological separation apparently precludes the formation of hybrids between them. In contrast, subsp. *marginata* hybridizes with subsp. *navajoensis* at many localities in this region. The combined distribution of four characters, maximum leaf length, floral tube length, pubescence type (villous versus hirsute), and features of the capsule considered collectively were used to detect putative hybrids (Fig. 117). Only the putative hybrid plants that are morphologically closer to subsp. *navajoensis* (closed triangles) are included here, whereas other plants more similar to subsp. *marginata* are discussed under that subspecies. Plants of the first kind are the more common than those of the second kind.

The majority of these putative hybrids seem to represent sporadic recent hybridizations with the parents remaining distinct, but a few, especially some of those from the geographical periphery of *Oenothera caespitosa* subsp. *navajoensis,* may represent stabilized hybrid derivative populations that have become established in the distinctive habitat.

Hybrids can be found throughout the area where *Oenothera caespitosa* subspp. *navajoensis* and *marginata* occur together (see Fig. 117). Most populations containing hybrids occur in geologically complex areas common in the Colorado Plateau where subsp. *marginata* occurs on the tops of the plateaus in loose sandstone-derived soils in pinyon-juniper woodlands, and subsp. *navajoensis* below in the shales and clays of the canyons and plains. We do not at present have detailed information on the number of hybrids relative to the parents in populations nor their ecological distribution, but judged from the available collections where a few hybrids have often been collected mixed with larger numbers of one parent or the other (e.g., Kane Co., Utah, *Morris et al. 160*), they seem to occur only sporadically. One population from Kaiparowits Plateau, Kane County, Utah (*Atwood & Trotter 5269*) is morphologically intermediate between these two subspecies, but we have not seen any collection of either parent from that area. Moreover, this population is from an elevation of 2,300 m, several hundred meters higher than the known upper altitudinal limit of subsp. *navajoensis.* It is therefore tentatively interpreted as representing a stabilized hybrid derivative. Based on intermediate characteristics another plant, *Harrington 3925,* from a population in Moffat County, Colorado, perhaps also represents an independently derived stabilized hybrid population. It is largely because of the presence of these presumably independently derived stabilized intermediate populations that the rank of subspecies has been given to *navajoensis.*

Hybrids involving subsp. macroglottis. Among the members of the *Oenothera caespitosa* complex, the range of *O. caespitosa* subsp. *macroglottis* overlaps with that of *O. caespitosa* subspp. *caespitosa, marginata, navajoensis* and *O. harringtonii,* but it apparently intergrades only with subsp. *marginata.* Plants of *O. caespitosa* subsp.

marginata growing in alluvium between Clark and Seedhouse in the Elk River Valley, Routt County, Colorado (*Weber 6945, Wagner 4046*) had capsules with features similar to those of subsp. *macroglottis*; leaves of some individuals resemble those of subsp. *macroglottis* while the leaves of others are narrower and more lobed as in subsp. *marginata*. From there westward at progressively lower elevations, populations appear gradually to take on more characteristics of subsp. *marginata* (e.g., Routt Co., Colorado, *Wagner 4047*, Moffat Co., Colorado, *Wagner 4048*, both included under subsp. *marginata*). Judging from other collections, subsp. *marginata* intergrades completely with subsp. *macroglottis* in many of the relatively limited areas where they come in contact. Such complete intergradation occurs in these populations at intermediate elevations, and the two subspecies are not strongly isolated edaphically: both grow in coarse-textured soils derived from igneous rocks or sandstones. In contrast, hybrids between subspp. *macroglottis* and *navajoensis* have not been found, presumably because of their considerable spatial separation and strongly differing edaphic requirements. For example, in the eastern portion of the Colorado Plateau (west-central and southwestern Colorado) where they both occur, subsp. *navajoensis* grows in low-elevation xeric scrub communities whereas subsp. *macroglottis* grows in forest communities at higher elevations of the plateaus or in the nearby mountains.

There is some evidence (discussed on p. 41) that suggests that *Oenothera caespitosa* subsp. *macroglottis* has hybridized in the past with subsp. *caespitosa*, producing a long-haired form in eastern Wyoming which is included in subsp. *caespitosa*. Study of several sites within their area of geographical overlap in northern Colorado, however, did not reveal any conclusive proof of hybridization. Textural analysis of soils from one population growing on a slope with bigsage-Gambel oak scrub in Routt County, Colorado (*Wagner 4041*), however, showed that the population was growing in a clay-loam with 30% sand, 35% silt, and 35% clay, a soil much lower in sand than the typical 70–90% sand found by Goeken (1968) in other sites where subsp. *macroglottis* grew. The soil at this site resembled soils where populations of subsp. *caespitosa* occurs in its sand content. The four or five hundred plants examined in the population, however, were all morphologically typical of subsp. *macroglottis*.

3. Plants from the Kaibab and Coconino Plateaus southeast along the upper elevations on the north slope of the Mogollon Rim and south to Cochise County in Arizona, as well as populations in adjacent New Mexico, have nearly sessile capsules, very broad buds, and slightly asymmetrical capsule bases, as in *Wagner 3793* (MO) from near Flagstaff, Coconino County. These features are suggestive of *Oenothera caespitosa* subsp. *macroglottis* but the plants, although more similar to subsp. *marginata*, may represent hybrid derivatives involving these two subspecies.

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